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# An Extension of the Coefficient of Divergence for Use with Multiple Characters

PHILIP J. CLARK

AS a measure of the divergence existing between two populations with respect to some given character, Klauber (1940) has suggested that the difference between the means of the two populations be divided by the average of the means. This measure has the advantage that it is independent of the units in which the character is recorded. The definition of divergence provided by Klauber is subjective, to the extent that other definitions of the term can easily be obtained. The value of this definition is that it enables the amount of divergence between two populations to be objectively estimated. Formulas, or definitions, constructed in such a manner as to make objective evaluation possible are much to be desired in biological work, for they provide standards which make agreement among workers possible. This paper suggests a slight modification of Klauber's formula and provides a generalization of the formula for the simultaneous treatment of any number of characters.

Let $A$ and $B$ represent two populations, and let $Q_1$ represent some particular character. Let $\bar{A}_1$ and $\bar{B}_1$ denote the mean values of character $Q_1$ in populations $A$ and $B$, respectively. Then Klauber's coefficient of divergence (C.D.) between populations $A$ and $B$ with respect to $Q_1$ is:

$$C.D. = \frac{2(\bar{A}_1 - \bar{B}_1)}{(\bar{A}_1 + \bar{B}_1)}. \qquad (1)$$

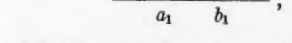
In absolute value this coefficient may range from 0 to 2. For many purposes a coefficient ranging between 0 and 1 is more convenient, and this is easily achieved in the present situation by dropping the factor 2 from the numerator. The coefficient of divergence is then defined as:

$$C.D. = \frac{\bar{A}_1 - \bar{B}_1}{\bar{A}_1 + \bar{B}_1}. \qquad (2)$$

In other words, the coefficient of divergence, by this definition, is the difference between the means divided by the sum of the means. If the coefficient of divergence is defined as here proposed, it may now be written as:

$$\text{C.D.} = a_1 - b_1, \qquad (3)$$

where $a_1 = \dfrac{\bar{A}_1}{\bar{A}_1 + \bar{B}_1}$ and $b_1 = \dfrac{\bar{B}_1}{\bar{A}_1 + \bar{B}_1}$. The values of $a_1$ and $b_1$ can be plotted in one-dimensional space as below:

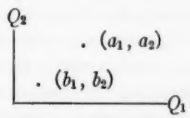



and the divergence between populations $A$ and $B$ with respect to $Q_1$ is the distance between the points $a_1$ and $b_1$.

This may now be extended to include the simultaneous consideration of a second character. Let $Q_2$ represent this second character, and let $\bar{A}_2$ and $\bar{B}_2$ denote the mean values of $Q_2$ in populations $A$ and $B$, respectively. The divergence between the two populations with respect to $Q_2$ may be written as:

$$a_2 - b_2, \qquad (4)$$

where $a_2 = \dfrac{\bar{A}_2}{\bar{A}_2 + \bar{B}_2}$ and $b_2 = \dfrac{\bar{B}_2}{\bar{A}_1 + \bar{B}_2}$. The pair of two-dimensional points, $(a_1, a_2)$ and $(b_1, b_2)$, may then be taken to represent populations $A$ and $B$ respectively, with respect to characters $Q_1$ and $Q_2$ simultaneously. These points may be plotted in this manner:

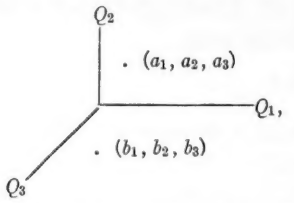



The distance between these points will represent the divergence between populations $A$ and $B$ with respect to characters $Q_1$ and $Q_2$ and may be derived from the formula:

$$\sqrt{(a_1 - b_1)^2 + (a_2 - b_2)^2}. \qquad (5)$$

If we now wish to introduce a third character, $Q_3$, we can form $a_3$ and $b_3$ as above. The

three-dimensional points, $(a_1, a_2, a_3)$ and $(b_1, b_2, b_3)$, can now be diagrammed as follows:




and the distance between these points will represent the divergence between populations $A$ and $B$ with respect to $Q_1$, $Q_2$ and $Q_3$. In this case the distance is equal to

$$\sqrt{(a_1 - b_1)^2 + (a_2 - b_2)^2 + (a_3 - b_3)^2}. \quad (6)$$

In this manner it is possible to consider a large number of characters. If we have $k$ characters, $Q_1, Q_2, Q_3, \cdots, Q_k$, the divergence between populations $A$ and $B$ will be represented by the distance between the $k$-dimensional points $(a_1, a_2, \cdots, a_k)$ and $(b_1, b_2, \cdots b_k)$, which is

$$\sqrt{(a_1 - b_1)^2 + (a_2 - b_2)^2 + \cdots + (a_k - b_k)^2}. \quad (7)$$

Since the maximum distance between such $k$-dimensional points is $\sqrt{k}$, we divide the above expression by $\sqrt{k}$ to obtain a $k$-dimensional coefficient of divergence:

$$C.D. = \sqrt{\frac{(a_1 - b_1)^2 + (a_2 - b_2)^2 + \cdots + (a_k - b_k)^2}{k}} \quad (8)$$

whose absolute value ranges between 0 and 1.

The utility of the $k$-dimensional coefficient of divergence will be demonstrated by applying it to a group of animals whose relationships are well known. The objective is to determine to what extent the simultaneous treatment of a number of relatively inconsequential characters will reproduce these relationships. Consequently diagnostic characters are deliberately omitted in this example. In the application of the coefficient of divergence to an unsolved problem it is recommended that more fundamental characters be chosen. Let

*A* denote a sample of 34 *Heterodon contortrix* from Kansas

*B* denote a sample of 64 *Thamnophis eques* from Arizona

*C* denote a sample of 218 *Natrix s. sipedon* from Michigan

*D* denote a sample of 94 *Natrix s. picti-ventris* from Florida

*E* denote a sample of 173 *Storeria dekayi* from Michigan

*F* denote a sample of 70 *Coluber c. constrictor* from Florida

*G* denote a sample of 66 *Coluber c. flaviventris* from Michigan,

and let

$Q_1$ represent the number of supralabial scales
$Q_2$ represent the number of infralabial scales
$Q_3$ represent the number of preocular scales
$Q_4$ represent the number of postocular scales
$Q_5$ represent the number of posterior temporal scales.

Our example contains, therefore, seven populations whose divergence from one another with respect to five superficial head-shield characters is to be estimated. If each population is compared with every other population in this collection, we shall have twenty-one separate coefficients of divergence. When arranged in order of ascending magnitude, the coefficients of divergence, computed from the means of the characters for the populations involved (Table I), appear as follows:

| | |
|---|---|
| CD .013 | subspecies vs. subspecies of *Natrix sipedon*. |
| FG .014 | subspecies vs. subspecies of *Coluber constrictor*. |
| BC .047<br>BD .057 | *Thamnophis eques* vs. *Natrix sipedon*. |
| BE .126 | *Thamnophis eques* vs. *Storeria dekayi*. |
| CE .133<br>DE .135 | *Natrix sipedon* vs. *Storeria dekayi*. |
| EG .155<br>EF .157 | *Storeria dekayi* vs. *Coluber constrictor*. |
| CF .176<br>BG .176<br>BF .177<br>CG .178<br>DF .180<br>DG .183 | *Thamnophis eques* and *Natrix sipedon* vs. *Coluber constrictor*. |
| AF .258<br>AG .260<br>AC .289<br>AD .293<br>AB .301<br>AE .352 | *Heterodon contortrix* vs. *Thamnophis eques*, *Natrix sipedon*, *Storeria dekayi*, and *Coluber constrictor*. |

In this enumeration a number of relationships are apparent. For example, *Heterodon contortrix*, of the Xenodontine complex, is seen to be more divergent from all of the other populations than any of these are from each other. Furthermore, *Coluber constrictor* is found to be more divergent from any of the so-called Natricines than any of these are from each other. Likewise, within the latter group, *Thamnophis eques* is more divergent from *Storeria* than it is from *Natrix*. Discontinuities in this tabulation clearly indicate the existence of the five primary groups: *Thamnophis*, *Natrix*, *Storeria*, *Coluber* and *Heterodon*, and the fact that these groups are not of equal rank is also shown. In this instance the coefficient of divergence has yielded results which are consistent with herpetological experience.

TABLE I

DATA FOR COMPUTATION OF COEFFICIENTS OF DIVERGENCE

| Populations | Characters | | | | |
|---|---|---|---|---|---|
| | $Q_1$ | $Q_2$ | $Q_3$ | $Q_4$ | $Q_5$ |
| $\bar{A}_i$ | 8.000 | 10.059 | 4.000 | 4.206 | 3.941 |
| $\bar{B}_i$ | 7.969 | 10.078 | 1.016 | 3.078 | 2.250 |
| $\bar{C}_i$ | 8.005 | 9.968 | 1.032 | 2.853 | 2.739 |
| $\bar{D}_i$ | 7.989 | 10.043 | 1.000 | 2.761 | 2.830 |
| $\bar{E}_i$ | 6.948 | 7.018 | 1.018 | 2.081 | 1.943 |
| $\bar{F}_i$ | 7.086 | 9.043 | 2.000 | 2.029 | 2.100 |
| $\bar{G}_i$ | 7.076 | 8.831 | 2.000 | 2.091 | 2.000 |

Means of characters $Q_1$ to $Q_5$ for populations *A* to *G*

In this coefficient, as in Klauber's one-dimensional coefficient, characters are weighted in inverse proportion to the sum of the means of the character in the two populations. If additional weighting is desired, a set of weights may be determined such that the $i$ th character is given a weight of $w_i$, where $0 \leq w_i \leq 1$. A weighted $k$-dimensional coefficient of divergence may then be defined as

$$C.D. = \sqrt{\frac{w_1^2(a_1 - b_1)^2 + w_2^2(a_2 - b_2)^2 + \cdots + w_k^2(a_k - b_k)^2}{k}} \quad (9)$$

This coefficient, subject to the restriction imposed on the $w_i$, also ranges between 0 and 1. In this paper, however, no attempt is made to define or use such a set of weights.

Caution should be used in drawing evolutionary or phylogenetic conclusions from coefficients of divergence. The coefficient of divergence is a measure of the difference between populations, but it will not distinguish lack of divergence from evolutionary convergence. It is possible, therefore, to obtain small divergence values between populations which are phylogenetically quite distinct. When one is interested in estimating evolutionary divergence, therefore, characters in which convergence has occurred should be omitted. The lower the taxonomic level, the less likely the influence of convergence and the more likely the assumption that similarity is primary rather than secondary. The application of the coefficient of divergence, consequently, will be most useful for groups of low level, particularly those of infraspecific level. Its use to determine relationships between groups which are as diverse as those used in the example in this paper will generally be hazardous.

The $k$-dimensional coefficient of divergence could be of use in zoogeographic studies of a single species. Samples can be obtained from various stations over the range of a species, and the divergence between these stations can be estimated. In this way, more accurate estimates of the evolutionary effects of various sorts of barriers can be made than have been available in the past. It is possible that the greatest use of the coefficient of divergence will be in studies of this sort.

No adequate statistical technique is available for assigning fiducial limits to the $k$-dimensional coefficient of divergence, but Hotelling's (1931) generalized $t$-test may be used to determine whether any coefficient differs significantly from zero. The disadvantage of being unable to assign fiducial limits can be partially offset by using large samples only. But, unfortunately, no objective method is now available for determining just how large the samples need be.

It should be mentioned that a definition of divergence that is in many respects more useful than the one described here can be obtained from discriminant analysis. The discriminant method has the advantage of considering the within group as well as the between group variability of the populations, and, furthermore,

fiducial limits can be obtained. But the amount of computation involved in applying such a method to any considerable number of populations with respect to more than a few characters is almost prohibitive with the usual type of computational equipment; and the present method is recommended as a rapid approximation to what might be obtained by this more rigorous method.

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Hotelling, H. 1931. The generalization of Student's ratio. *Ann. Math. Stat., 2: 360–78.*

Klauber, L. M. 1940. Two New Subspecies of *Phyllorhynchus*, the leaf-nosed snake, with notes on the genus. *Trans. San Diego Soc. Nat. Hist., 9: 195–214.*

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# Quadrupedal and Bipedal Locomotion of Lizards

Richard C. Snyder

SINCE the appearance of previous work on the bipedal running of *Basiliscus basiliscus* (Snyder, 1949), the motion picture analysis method of studying locomotion has been applied to several species of lizards. High speed motion pictures were taken of *Amphibolurus cristatus* (Agamidae), *Crotaphytus c. collaris*, *Gambelia w. wizlizenii* and *Sceloporus u. undulatus* (Iguanidae), and *Cnemidophorus t. tessellatus* (Teiidae). Quadrupedal locomotion of all species was photographed as well as the bipedal running characteristic of *Amphibolurus*, *Crotaphytus* and *Gambelia*.

Motion picture photography of running lizards presents several problems. Standard motion picture cameras operating at a maximum speed of 64 frames per second are inadequate to cope with the rapid leg action of the animals and when separate frames are projected for analysis, detail is greatly obscured, particularly in regard to position of the feet. Consequently, photography was done with an Eastman Kodak 16 mm. High Speed Camera equipped with a Kodak Anastigmat 63 mm. f/2.7 lens. Fifty-foot spools of Cine-Kodak Super X panchromatic reversal film were used exclusively.

Since it was necessary to provide at least a three-foot running area, and since the high camera speed requires intense illumination, nine reflector photospot lamps were mounted to cover the running track about two feet from the sand on which the lizards ran. It was necessary to place a sheet of heavy, heat absorbing glass between the lights and the running track; otherwise the sand rapidly became too hot for the lizards to tolerate. With this lighting arrangement good results were obtained with a camera speed of between 1000 and 1500 frames per second (exposure time per frame between 1/5000 and 1/5500 second), a speed adequate to fix leg and foot motion completely. Tests made at higher speeds resulted in underexposure. Increasing the illumination by concentrating three or more photospots at any one point solved the underexposure problem but created a new one; the lizards would not perform in such brilliant light.

The basic factors influencing the gaits of quadrupedal mammals as well as descriptions of the types of gaits employed have been clearly set forth by Howell (1944) and his assumption that the speed gait of lizards is the trot has been verified by the present studies. The description of quadrupedal locomotion to follow applies basically to all of the five species studied. The action of a hind leg illustrates the basic pattern of movement for all four appendages. The propulsive stroke begins when the foot strikes the ground, at which time the foot and shank are extended and the femur is flexed. As the cycle proceeds, the leg moves backwards with the foot progressively flexing on the shank, and the shank and thigh extend until the segments of the leg are in nearly a straight line. During the greater part of the stroke, the foot is plantar-flexed in

order to transmit the force of the thrust to the ground. The recovery stroke begins when the foot leaves the ground and the thigh and shank are flexed. As thigh flexion continues, the shank and foot are swung forward but are not further flexed and as the leg is protracted far forward, the thigh flexes maximally and is adducted while the shank and foot are partially extended. Subsequent extension of the shank returns the foot to the ground.

After the left foreleg strikes the ground, the left hind leg swings through its recovery arc (Figs. 4, 5, 6) and strikes the ground in advance of the right front leg (Fig. 7). The sequence of limb action (support pattern) is right hind—left front—left hind—right front. The hind feet come in contact with the ground at the same level, or in advance of, the ipselateral forefeet (Figs. 2, 6) but laterad to them. An exception to this is noted in *Gambelia* in which

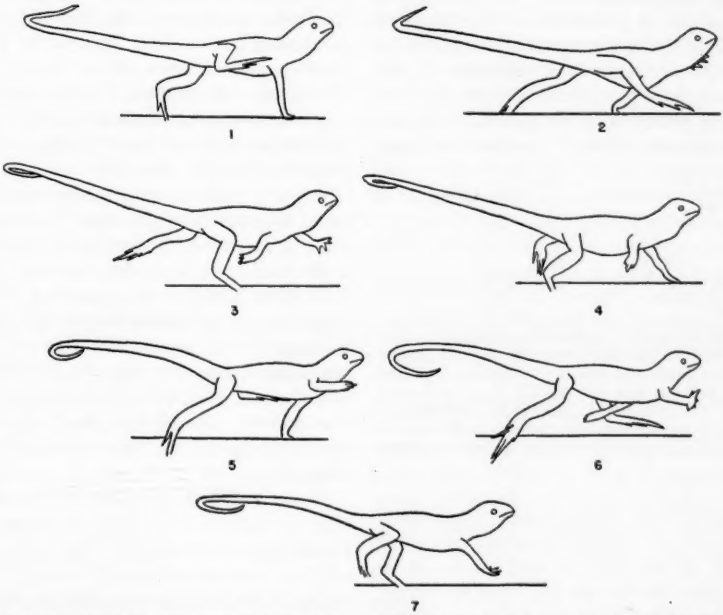



Fig. 1–7. Quadrupedal locomotion of *Crotaphytus c. collaris*. Locomotor cycle in sequence. Details of position of distal digits partially obscured by substrate. Made from motion picture by projection; camera 8 inches above substrate.

A complete locomotor cycle of *Crotaphytus* consists of several phases. At the onset of the quadrupedal run, both hind legs participate in the initial backward thrust, one of them being extended with greater force than the other. In the case illustrated (Figs. 1–7), the right hind leg participates with greater power than the left, thrusting the body slightly to the left and forward over the pivotal left front leg. With the completion of the backward thrust of the left hind leg, the right hind leg begins its recovery phase and is swung laterad and forward (Fig. 1) to contact the ground well in advance of the left front leg (Figs. 2, 3). the hind feet are swung around the forelegs to strike the ground on a line with, but in front of, the forefeet. The hind legs of *Sceloporus* and *Cnemidophorus* are not swung as far forward as in the bipedal species and the hind foot strikes the ground behind the level of the forefoot; both stride and recovery of the hind leg are considerably shorter in extent. In all forms studied, the hind foot meets the ground in the plantigrade position. The contralateral hind and forefoot occasionally hit the ground simultaneously (as in the trotting horse) but in the usual mode of progression the hind foot almost always touches the ground before the

forefoot (Figs. 3, 7). The front legs strike the ground partially flexed, and on the downstroke of their recovery the digits are widely abducted (Figs. 3, 6). The body and the bulk of the tail are carried free of the ground, or the tail tip may drag. *Cnemidophorus* customarily carries the body and tail lower than do the other species and the pelvis, tail base and tail may drag.

The footfall formulas of quadrupedally running lizards (Fig. 8) show clearly that the basic pattern of limb action is the trot. Body support is, for the most part, maintained by the action of diagonally opposite legs. It has previously been pointed out that the hind foot comes in contact with the ground in advance of the opposite forefoot. As speed increases,

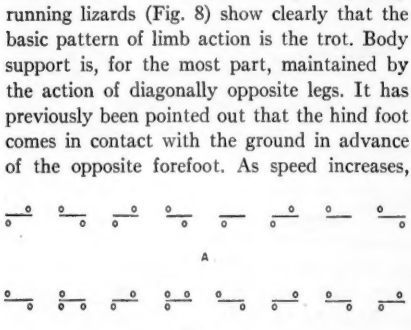


Fig. 8. Footfall formulas of quadrupedal locomotion of lizards. The feet in contact with the ground at any one phase are indicated by circles. Direction of progression is from left to right. A, two phases of the trot characteristic of *Crotaphytus*, *Gambelia* and *Amphibolurus*; B, diagonal running walk characteristic of all species becoming a trot at higher speed.

the length of time of body support on the hind legs increases as the lizard lengthens the stride (Fig. 8, A), for, since the hind legs are much longer than the forelegs, the latter are unable to match them stride for stride. At slower speeds, a type of diagonal "running walk" is employed (Fig. 8, B) which blends into the trot as the length of stride is augmented. It is evident that these lizards can employ the walk (in which there are phases when all four feet are in contact with the ground), the running walk and the trot, depending on the speed of progression, and that the rapid trot (Fig. 8, A) merges into a bipedal gait in certain long limbed, heavy tailed lizards which are capable of this type of locomotion. It is also notable that at any speed above the walk, the front legs are never in simultaneous contact with the ground as they are in certain asymmetrical gaits of mammals such as the canter and gallop (Howell, 1944). This indicates that body support during locomotion is a primary function of the hind limbs and that walking, trotting and bipedal running of lizards are essentially symmetrical forms of locomotion.

The time sequence of limb action shows that not only does the hind foot strike the ground before the diagonally opposite forefoot, but that it also leaves the ground in advance of the forefoot. At the beginning of recovery of the hind leg, body support is largely a function of the opposite hind leg which is beginning its propulsive stroke, and, to a lesser degree, of the foreleg on the same side. During recovery, the foreleg is not lifted clear of the ground directly; as momentum carries the body over the foreleg, that member loses its supportive function and is dragged along the ground until the contralateral hind foot is halfway through its recovery phase. Thus, for a short period of time, body support rests on front and hind leg of the same side as it does in pacing animals, a factor which contributes materially to the lateral rotation of the entire body as the lizard runs. This type of leg action is particularly apparent in *Cnemidophorus;* the front leg is dragged for a considerable period of time, beginning its recovery when the contralateral hind leg has been protracted forward more than halfway, thus allowing the diagonal feet to come in contact with the ground at the same instant.

The action of the hind legs during quadrupedal running is essentially the same as in bipedal progression (Snyder, 1949). Both front and rear legs describe wide, sweeping arcs during stride and recovery and the proximal leg segments move primarily in the horizontal rather than the sagittal plane. There is little tendency toward the pendulum type of leg action characteristic of cursorial mammals in which the appendages swing directly forward and backward. In long legged species such as *Amphibolurus*, *Crotaphytus* and *Gambelia*, the hind foot strikes the ground with the toes pointing directly anterior or at an angle up to twenty degrees laterad of anterior. In *Sceloporus* and *Cnemidophorus* the hind feet toe out laterally to a much greater extent, usually not less than fifty degrees and commonly more from a line marking the long axis of the body. As the hind leg moves through the propulsive stroke, the foot rotates laterally on the ground with the direction of thrust progressively sidewards

and backwards, a phenomenon previously noted in *Anolis* (Schaeffer, 1941: 440). There is a definite plantar flexion of the foot which contributes to propulsion and the digits are abducted for maximum surface contact with the ground. During recovery, both front and hind legs are raised and swung laterally while the feet are pronated medially in order to gain position for striking the ground. The action of both pairs of appendages is similar to that of *Triturus* (Evans, 1946; Schaeffer, 1941) except that movement is much more rapid and that the amphibian does not pronate the feet.

As Schaeffer (1941: 446) has pointed out, the recovery phase of the reptilian (crocodilian) limb is relatively simple compared to the amphibian (urodele) due to the medially directed femoral head which allows the femur (and thus the entire leg) to move in a more nearly vertical plane. It may be noted here that the larger relative size of the lacertilian internal trochanter effectively limits the degree to which the femur can act in a vertical plane and that this degree is less than in *Alligator*. Even if it were possible for lizards to bring the femur into a vertical plane, the construction of the dorsal rim of the acetabulum offers less support in lizards for stresses transmitted through the femur to the pelvic girdle. (This and other topics concerning the skeletal and muscular basis for locomotion will be the subject of further work.)

The extent to which the front legs participate in quadrupedal locomotion varies with the species, the speed of progression and with the ability to run bipedally. The forefeet are plantigrade in action in *Sceloporus* and *Cnemidophorus* and the thrust of the leg is dorsal and posterior as the body is raised and pushed forward. In *Amphibolurus*, *Crotaphytus* and *Gambelia* the front feet are digitigrade at any speed above that of a walk; the forelegs function as momentary supports for the anterior part of the body and most of their thrust is transmitted dorsally. When running at full speed, *Sceloporus* exhibits a definite tendency toward reduced propulsive action of the front legs and the feet strike the ground in the digitigrade manner. Sand tracks of other species such as *Uma notata*, *Holbrookia texana* and *Sceloporus magister* indicate a reduced role of the forelegs in locomotion and there is every reason to suspect that an increase in hind leg length coupled with a heavier tail in such forms might well lead to the adoption of a bipedal gait. In fact, Howell (1944: 244) has pointed out that bipedal locomotion of lizards may have evolved in this fashion. In all species studied, the forefeet swing well toward the mid-ventral line before contact with the ground is made and are then moved laterally to strike the ground. The front legs are spread more widely in *Sceloporus* and *Cnemidophorus* than in the other genera.

The body movements parallel the hind leg movements in that the trunk bends horizontally to the same side as the hind leg which is being protracted. The degree of flexion is greatest when the hind foot strikes the ground at the onset of the propulsive stride. Coupled with horizontal bending is a considerable degree of rotation of the body around its long axis, which, as previously explained, is caused by the nature of the locomotor cycle. The degree of body rotation is increased during bipedal locomotion. Both flexion and rotation of the body in the direction of the protracted hind leg serve to lengthen the stride and the extent of both flexion and stride increases with the speed of progression. The position of the head and neck remain relatively the same during locomotion, indicating compensatory movements for the action of the trunk which prevent lateral oscillation of the head. As Howell (1944: 122) has pointed out, a heavy head will not interfere with a symmetrical gait if the neck is short.

Bipedal locomotion of *Amphibolurus*, *Crotaphytus* and *Gambelia* is essentially the same as that of *Basiliscus* (Snyder, 1949). These lizards are able to assume the bipedal gait directly from a resting position or from slow or rapid quadrupedal progression. There is a not very pronounced tendency for the action of the hind foot to become digitigrade during rapid bipedal running. While moving on the hind legs, *Crotaphytus* inclines its body at about a 45-degree angle and the front legs are partially flexed and held with the toes pointing forward; there is very little swinging of these members. When running at full speed, the lizard is able to accomplish a stride approximately three times the body length (snout to vent). The observed maximal length of the bipedal stride of *Amphi-*

*bolurus* is 2½ times the body length. In both species, length of stride is variable and increases with the speed. The body of *Gambelia* is held erect at a 75-degree angle, an extent not approached by other bipedal lizards thus far observed.

From the point of view of muscular work involved, there is little doubt that bipedal locomotion is a more efficient type of rapid progression in lizards than quadrupedal. By far the greater part of the propulsive force in moving the body forward is accomplished by the hind legs in either type of movement. It is probable that in traversing any given distance the energy expenditure for leg recovery alone is greater in quadrupeds than in bipeds. As

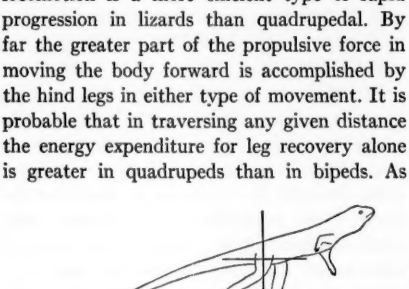
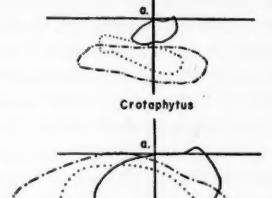
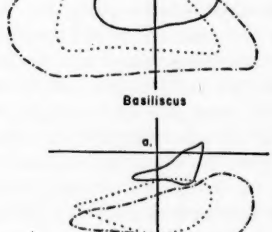


Fig. 9. Bipedal locomotion of *Amphibolurus cristatus*. Perpendiculars drawn through acetabulum. *Upper*, body raised high off ground, feet nearer mid-ventral line; *lower*, body carried near ground, feet farther from mid-ventral line. Made from motion picture by projection.

shown by Barclay (1946: 189), length of stride is proportional to length of leg and the distance through which the acetabulum moves during the time that the feet are not in contact with the ground. The less the feet are needed in contact with the ground, the easier it is to increase the length of stride and decrease the frequency of moving the limbs. This, in turn, tends to decrease the energy needed to move the limbs, for the energy necessary to contract muscles is increased as the speed of action is increased.

Studies of the bipedal locomotion of the agamid *Amphibolurus* indicate that in some respects its ability to progress in this fashion is better developed than in iguanid lizards. The head and trunk may be inclined at a 25-degree angle from the horizontal with the tail tip dragging or the body and tail may be carried parallel to the ground with the head and neck upraised (Fig. 9). Furthermore, the body as a whole may be carried at variable heights from the ground depending upon the degree of leg and thigh flexion during the locomotor cycle. Examination of Fig. 9 shows that *Amphibolurus* is able to run bipedally in much the same fashion as *Basiliscus*, or, by keeping the leg extended to greater lengths throughout the cycle, it is able to run with the entire body held considerably higher off the ground. A



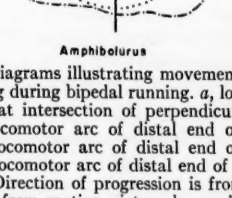




Fig. 10. Diagrams illustrating movements of the right hind leg during bipedal running. *a*, location of acetabulum at intersection of perpendicular lines; *solid line*, locomotor arc of distal end of femur; *dotted line*, locomotor arc of distal end of shank; *broken line*, locomotor arc of distal end of metatarsals (foot). Direction of progression is from left to right. Made from motion picture by projection.

notable advantage of the latter method is that the feet strike the ground closer to the mid-ventral line and the amount of lateral swinging of the leg and foot during recovery is reduced (Fig. 10). This adaptation, which results in a more pendulum-like action of the leg, is of distinct advantage to a cursorial animal in that it improves the leverage exerted by the leg segments during propulsion and reduces the energy required for recovery. The amount of body rotation during bipedal running is less than in any iguanid studied. The hind feet strike the ground pointed laterally at a 30-degree angle and remain in this position

throughout the propulsive cycle without rotating on the ground.

During the locomotor cycle, the distal end of the femur describes an ellipse that is almost equidistant craniad and caudad of a perpendicular drawn through the acetabulum (Fig. 10). The major portion of the ellipse formed by the thigh of *Amphibolurus* lies forward of this perpendicular. The principle muscles involved in protracting the leg as a unit are the coxofemoral flexors and the nature of the ellipse indicates that energy requirements for the recovery of the leg are relatively less than in the other species. Additional evidence may be found by comparing the posterior portions of the ellipses formed by the distal ends of the thigh, shank and foot. In *Amphibolurus*, there is considerably less dorsal and lateral swinging of the leg segments at the onset of and during recovery. Further, whereas in the iguanid species the major portion of the propulsive thrust of shank and foot lies posterior to the acetabulum, in *Amphibolurus* this phase takes place in an area more equidistant anterior and posterior to the acetabulum, a fact which is in part explained by the more anterior position of the thigh during the entire cycle.

During bipedal locomotion, the forelegs may be carried partially flexed, upper arm close to the body with the forearm and foot pendent, or the forelegs may be extended outward from the body and swung rhythmically. The foreleg swings down toward the ground at the time that the ipselateral hind foot strikes the ground; it is never moved in opposition to the motion of the contralateral hind leg as a compensatory action. It is evident that this type of motion is based upon the pattern of quadrupedal locomotion, thus tending to verify Howell's (1944: 219) statement that lizards cannot alter the sequence of their limb movements. The method of foreleg swinging used serves to increase the lateral rotation of the body, which in turn, brings the hind feet closer to the mid-ventral line, a cursorial advantage.

The ability to raise the forepart of the body from the ground while in a stationary position is possessed by several lizards, not all of which can be classed as truly bipedal species. During courtship, both *Calotes* and *Sitana* (Smith; 1935: 192, 146) stand erect, hind quarters supported by the tail base. Both *Basiliscus* and *Amphibolurus* can elevate the anterior part of the body while standing still; they have not been observed to maintain this position for more than a few seconds. Gadow (1901: 523) includes a picture of *Chlamydosaurus kingi* sitting on the base of the tail in the manner of a kangaroo. Several species of *Varanus* are capable of this type of action, and Loveridge (1934) illustrates the characteristic defensive attitude of *V. gouldii* in which a tripodal stance is assumed with the erect body balanced on the hind legs and tail.

A list of five iguanid and three agamid lizards that regularly resort to bipedal locomotion has been previously reported (Snyder, 1949: 130). To these may be added: Iguanidae; *Corythophanes cristatus* (Bogert, personal communication), *Gambelia w. wislizenii* (observed), *Dipsosaurus d. dorsalis* (observed). Agamidae; *Otocryptis weigmannii* (Smith, 1935: 147), *Sitana ponticeriana* (Smith, 1935: 145), *Physignathus cocincinus* (Smith, 1935: 237), *Calotes versicolor* (Smith, 1935: 192), *Amphibolurus rufescens* (Barrett, 1950: 40–41) and *Amphibolurus cristatus*, reported on here. According to Mitchell (personal communication), "The bipedal locomotion of *A. cristatus* has earned for it the local name of 'bicycle lizard'. ... *A. pictus* does not appear to run on its hind legs in the same style as *cristatus*, but is quite capable of standing erect.... I have long suspected from field observation, that when greatly activated, many other species of the genus *Amphibolurus* also resort to bipedal locomotion." Van Denburgh (1922: 508) states that *Cnemidophorus maximus* has been observed "running on the hind feet only, the front legs being held clear of the ground and the body raised at an angle." This is the only reference known to me of the bipedal habit in teiid lizards, although it is well known that they are capable of very rapid locomotion, particularly those species that forage on open ground. Barrett (1950: 59) comments upon the varanid lizard, *Varanus giganteus*, that is said to be bipedal at top speed. If true, this species is by far the largest lizard capable of this method of locomotion.

A survey of habitat preferences indicates that bipedal locomotion, or a tendency toward it, has been developed in two general groups of lizards. One category includes primarily

terrestrial species living in open, sandy or rocky areas where excursions are made on open ground. To this group belong all bipedal species of North America as well as *Amphibolurus*, *Chlamydosaurus*, *Sitana*, *Otocryptis* and, possibly, *Varanus giganteus*. The second category includes species that live in brushy or forested areas and may be classed as semi-arboreal, semi-aquatic or both. Included in this group are *Basiliscus*, *Corythophanes*, *Physignathus*, *Hydrosaurus* and *Calotes*.


## Summary and Acknowledgments

The basic pattern of limb action during quadrupedal locomotion of lizards is described. *Crotaphytus c. collaris* is used as a type.

Differences between lacertilian and mammalian locomotion are indicated.

Hind leg and body action of *Amphibolurus* during bipedal progression indicates a more efficient locomotor cycle than in bipedal iguanids.

A previous listing of eight species of lizards habitually resorting to bipedal locomotion is augmented by ten others, and is subdivided into two groups based upon general habitat preferences.


The writer is indebted to Dr. F. J. Mitchell of the South Australian Museum, Adelaide, Australia, who furnished several *Amphibolurus* for study, and to the Audio-visual Department, University of Washington, for loan of photographic equipment. This study was supported in part by the Fund for Research in Biology and Medicine derived from Initiative 171 of the State of Washington.

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# Pliocene Lizards from Kansas

John W. Twente, Jr.

THE lizards reported in this paper were collected in the summer of 1950 from Upper and upper Middle Pliocene deposits in southwestern Kansas.

I am greatly indebted to Dr. Claude W. Hibbard and Dr. Norman E. Hartweg of the University of Michigan and to Dr. Edward H. Taylor of the University of Kansas for advice and criticism and the use of specimens under their direction. Acknowledgement is also given to Dr. Rollin H. Baker and Dr. Robert W. Wilson of the University of Kansas Museum of Natural History for the privilege of observing specimens. The drawings were made by Mr. William L. Brudon.

### *Sceloporus robustus*, sp. nov.

(Figs. 1, 2, 3 and 4)

Holotype.—No. 27665, University of Michigan Museum of Paleontology. Left dentary with 17 teeth and spaces for seven others.

Paratypes.—No. 27666, a nearly complete left dentary with eight complete teeth and spaces for 14 to 16 more; No. 27668, a nearly

complete right dentary with 17 complete teeth and broken teeth or spaces for seven others; No. 27667, two fragmentary right dentaries, one with 13 and the other with nine complete teeth.

REFERRED MATERIAL.—No. 27669 consists of fragments of 17 dentaries referred to this species. These specimens were collected by the University of Michigan, Museum of Paleontology field party under the direction of Dr. Claude W. Hibbard.

HORIZON AND TYPE LOCALITY.—Upper Pliocene, Rexroad formation, Rexroad fauna. Locality UM-K1-47, Fox Canyon, XI Ranch, Sec. 35, T. 34S., R. 30W., Meade County, Kansas.

DIAGNOSIS.—A *Sceloporus*, apparently approximately the same size as a large *Sceloporus undulatus garmani* Boulenger, but the dentary is more robust and possesses a deep excavation on the posterior lateral surface for the insertion of what is interpreted to be the adductor mandibularis muscle. The teeth are relatively heavy and are somewhat transversely compressed at the base.

DESCRIPTION OF HOLOTYPE.—The holotype is a nearly complete left dentary 8 mm. in length bearing 15 complete teeth, 2 replacement teeth and spaces for 7 others. The teeth are typically iguanid in character, the trilobation being more evident in those in the posterior part of the jaw. The teeth appear to be well-worn in that the median cusp is worn down to the level of the lateral cusps in most instances. However, the replacement teeth show the median cusp to extend well above the lateral cusps. The teeth are compressed transversely and are approximately twice as thick at the base as at the tips and are strongly ankylosed to the outer dentary wall. The teeth in the anterior part of the dentary do not show the evidence of trilobation as do those in the posterior part (the first 13 tooth spaces counting from the most posterior). The tooth row is 6½ mm. in length and there are 20 teeth per half centimeter.

The meckelian groove (Fig. 2) is deep and well-developed extending to the symphysis. The shelf above is relatively heavy and protrudes a short distance mesially from the bases of the teeth. The part of the dentary ventral to the meckelian groove is very strong and forms the ventral part of the jaw. The meckelian groove faces ventrally at the symphysis and a short distance posterior to this it turns ventromesially becoming gradually mesial in position towards the posterior part of the dentary.

The labial face of the dentary (Fig. 1) shows

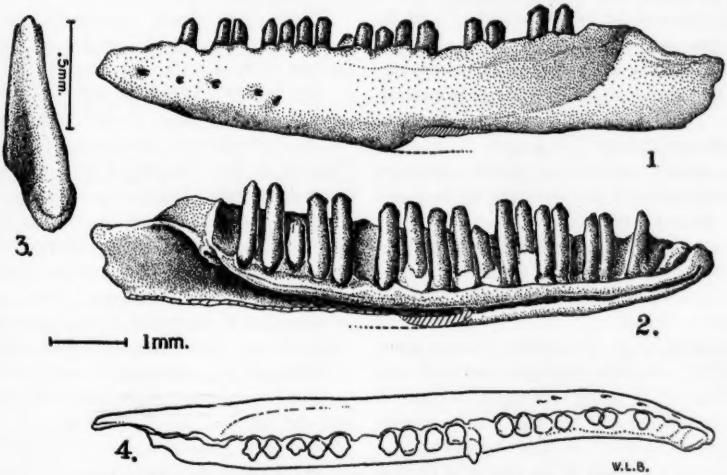


Fig. 1. Labial view of left dentary of *Sceloporus robustus* (No. 27665).
Fig. 2. Lingual view of same.
Fig. 3. Tooth showing trilobation and transverse compression at the base.
Fig. 4. Occlusal view of same.

four prominent foramina in the anterior one-third and a fifth foramen slightly below and behind the fourth which is situated at the level of the ninth tooth space from the symphysis. At the region of the last tooth, a distinct ridge extends downward and obliquely towards the anterior part of the jaw. This ridge forms the boundary of a deep excavation which extends to near the middle part of the dentary. This depression is interpreted to serve as the insertion of the adductor mandibularis muscle and is more prominent in *S. robustus* than in any of the recent scelopori surveyed. When viewed from the labial side, therefore, the dentary is slightly concave at its posterior half and becomes convex towards the anterior.

From an occlusal view (Fig. 4) the dentary is straight from the posterior border to approximately 2 mm. from the symphysis where the angle of curve occurs. The tangent of the angle whose opposite side is the chord connecting the symphysis and the beginning of the curve in the dentary has a value of four. The width of the dentary at the region of the most posterior tooth is 1 mm. The dentary gradually narrows toward the region of the angle where the measurement is ¾ mm.

Description of Paratypes.—These agree essentially with the holotype although the fifth foramen is better developed (except in No. 27666 where it is lacking) and is directly in line with the other foramina. A great amount of variation is evident in the degree of trilobation of the teeth, but this is presumably due to the amount of wear. No replacement teeth are present in any of the paratypes.

The depth of the excavation on the labial surface of the dentary is also variable, but the presence of this characteristic is always evident to the naked eye.

Comparisons.—These dentaries have been compared with those of all of the species of *Sceloporus* living in Kansas, Oklahoma, Texas, New Mexico, Arizona, Colorado and many of the forms living in México. Although the dentary is approximately the same size as that of the *Sceloporus undulatus* living in Kansas today, in *Sceloporus robustus* it is decidedly heavier. The teeth are transversely compressed at the base in the fossil form whereas those of *S. undulatus* are nearly conical at the base.

The meckelian groove is much more pronounced than in the living species and the part of the dentary above the groove is much thicker and heavier forming a definite shelf. In the recent forms studied only a very slight shelf is formed separating the base of the teeth from the mesial border of the dentary.

The labial surface of the dentary in the recent form is convex throughout showing little evidence of the excavation so prominent in *S. robustus*.

An occlusal view of the recent species shows that the curve towards the symphysis begins very near the middle part of the tooth row. In *S. robustus* this angle begins until very near the symphysis.

Discussion.—These specimens were referred to the family Iguanidae on the basis of the trilobate teeth. All of the living genera of this family which have members falling in this size group were studied and the fossil specimens could only be ascribed to the genus *Sceloporus*. This comparison was made on the basis of the type of teeth, the degree of trilobation and the number, and on the general characters of the dentary itself. Differences found in the fossil species were not deemed sufficient to warrant generic rank since a great amount of variation in characters of the dentaries and teeth occurs in the living species of *Sceloporus*.

Although *S. robustus* is a relatively small species it possesses weight and ruggedness of the dentary not found in living species of a similar size. *Eumeces striatulus* Taylor found in the same beds shows a similar degree of robustness in comparison to the species living today.

As far as I can determine, this is the first fossil record of the genus *Sceloporus*.

### *Eumeces striatulus* Taylor

*Eumeces striatulus* Taylor, 1941. *Kans. Geol. Surv. Bull.* 38: 171–72.

No. 27674 consists of a nearly complete right dentary with 19 complete teeth and spaces for four more; the anterior tip of a right dentary with ten teeth and spaces for two more; and a right maxillary containing 16 complete teeth and spaces for six more. These specimens were collected in association with the upper Middle Pliocene Saw Rock Canyon fauna (Hibbard, 1949) University of Kansas locality No. 6, Saw Rock Canyon, Sec. 36, T. 34S., R. 31W., Seward County, Kansas.

This is the first record of *Eumeces striatulus* Taylor from beds other than the type locality

(Rexroad formation, Upper Pliocene, Locality 2 [Taylor, 1941]). Although from beds somewhat older than the type locality, these specimens agree with the holotype in detail except that they are somewhat smaller. The complete right dentary is approximately one-half the size of the holotype and of other individuals of this species referred to in this paper, but it has been found that young individuals of living *Eumeces* differ from the adults (in characters of the jaws) only in size and the degree of wear on some of the teeth.

Hibbard (1949) has discussed the relationship of the Saw Rock fauna to the Rexroad fauna as follows:

> From a study of the vertebrates it is evident that the forms are younger than the Edson Quarry fauna (Hemphillian) from Sherman County, Kansas. A closer relationship is shown between the Rexroad fauna and the Saw Rock fauna than between the Saw Rock fauna and the Edson Quarry fauna, as indicated by the rodents. For this reason the fauna could be assigned either to the upper part of the Middle Pliocene or to the lower part of the Upper Pliocene.

Many specimens of *Eumeces striatulus* were also collected by Hibbard and party in 1950 from the same locality as *Sceloporus robustus*. A complete right dentary, No. 27659, has 21 teeth and spaces for two others. This is a better specimen than the holotype (Kansas University Museum of Vertebrate Paleontology No. 5079). Five fragmentary dentaries, No. 27661, and nine fragmentary maxillaries, No. 27660 were recovered with specimen No. 27659.

Although from a different locality than the holotype, these specimens, members of the Rexroad fauna, agree with the specimens described by Taylor (1941).

### *Eumecoides hibbardi* Taylor

*Eumecoides hibbardi* Taylor, 1941. *Kans. Geol. Surv. Bull.* 38: 173–74.

The posterior part of a right dentary, No. 27663, containing the last ten teeth belongs to the above species. This specimen was found associated with *Sceloporus robustus*. It agrees with the holotype of *E. hibbardi* in the character of the teeth and the fact that the labial face of the dentary is concave. No other specimens of this species were found.

### *Eumecoides mylocoelus* Taylor

*Eumecoides mylocoelus* Taylor, 1941. *Kans. Geol. Surv. Bull.* 38: 174–76.

The posterior part of a right dentary, No. 27664, containing seven teeth and spaces for three more of *E. mylocoelus* was found associated with the other lizards from the Fox Canyon locality. Only one fragment of this species was collected. The labial face of the dentary in this form is convex as opposed to the concave condition found in *E. hibbardi*. (See Taylor, 1941, for a key and figures of both of these species of *Eumecoides*.)

The saurian members of the Rexroad fauna now include four genera and five species. One form, *Cnemidophorus bilobatus* Taylor has not been found to date at the Fox Canyon locality.

The Rexroad fauna is one of the best known fossil faunas in North America. Taylor (1941 and 1942) has studied the lizards and amphibians; Wetmore (1944) and Tordoff (1951) the birds; and Hibbard and Riggs (1949) and Hibbard (1941 and 1950) the mammals. Baker (1938) and Franzen and Leonard (1947) have recorded the mollusks. The paleoecology of the Rexroad fauna is discussed by Hibbard (1950: 175–178).

This paper is a contribution from the Musuem of Paleontology, University of Michigan.

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# A Louisiana Terrapin Population (*Malaclemys*)

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TURTLES of the genus *Malaclemys* occur in isolated populations along the Louisiana coast. Reports of fishermen indicate that in some localities they are exceptionally abundant and are often taken in nets. The demand for these turtles as food is now limited and they are not usually brought to market. The difficulty of collecting them without special equipment has discouraged their study by herpetologists.

The investigations of Hay, Hildebrand and others have contributed much to our knowledge of the life history of captive specimens but little information is available on natural populations. Too, most of the data reported on captives were derived from a study of a hybrid stock of two or three subspecies; *Malaclemys terrapin terrapin* (Schoepf) and *Malaclemys terrapin centrata* (Latreille), and of these two with *Malaclemys terrapin littoralis* Hay. It is difficult to relate the information so accrued to the existing populations.

Two subspecies are reported to occur on the gulf coast from the Florida panhandle to southern Texas, *Malaclemys terrapin pileata* (Wied) and *Malaclemys terrapin littoralis* Hay. The ranges of neither of these is adequately defined. The two subspecies are reportedly different in these respects (Hay, 1904; Carr, 1946):

| *M. t. pileata* | *M. t. littoralis* |
|---|---|
| Carapace black or dark brown. | Carapace lighter, brown |
| Plastron yellow, inclined to be dusky or olive. | Plastron nearly white. |
| Horny covering of upper jaw usually white but marked with dark color in the male. | Horny covering of upper jaw white in both sexes. |
| Legs, tail, skin of body nearly black. | Skin green-gray, thickly marked with black spots. |
| Sides of carapace nearly nearly parallel. | Sides of carapace not nearly parallel. |

A sample of 96 turtles from Dulac, Louisiana contains individuals having some of the characteristics of both these subspecies and others having the characteristics of each. The color variation is particularly striking. Some of the individuals are almost entirely black but others have a light gray carapace and a cream-colored plastron with gray legs and body skin on which numerous, well-defined black dots are evident. Many of the males have the black horny covering of the upper jaw characteristic of *M. t. pileata* but others have the jaw clear of dusky markings. There is no consistent, individual representation of the characteristics of either subspecies.

This population is tentatively considered to be an intermediate one. The characteristics are such, however, as to suggest that future investigations of the gulf coast populations will not justify their separation into two subspecies.

Of the 96 individuals, 70 were retained for study. This sample included 13 females and 57 males. All of the males and two of the females were sexually mature. This sex ratio of 4.4 males to one female is unusual in reptilian samples. The usual reported ratio is two or more females per male. The repeatedly reported preponderance of reptile females (Forbes, 1940) may be attributed to the difficulty of determining sex (Cagle, 1948) or to selective sampling. The large number of males in the present group may reflect the apparent tendency of females to move toward shore during the egg-laying season. Certainly it should not be assumed that this is the actual sex ratio. Hildebrand (1933: 241) stated that of 1,433 terrapins reared in captivity, 200 were identified as males and 1,233 as females when they were old enough to show sexual dimorphism. It is probable, however, that the 1,233 so-called females included many juvenile males that had not yet developed secondary sex characteristics.

The effect on natality of a disproportionate number of males and females in a reptilian population is possibly not so severe as has been demonstrated for bird and mammal populations. The ability of reptilian females to deposit fertile eggs for several seasons after copulation reduces the significance of the seasonal availability of males. It has not been demonstrated that courtship or copulation is essential to ovulation in reptiles.

The two mature females measured 17.6 and 17.7 cm. in plastron length respectively. The latter individual had 10 ovocytes larger than 15 mm. in diameter in the right ovary and 8 in the left. The smaller turtle had 9 ovocytes larger than 15 mm. in diameter in the right ovary and 5 in the left. No corpora albicans were present in either individual. On the assumption that these ovocytes represent the total number of eggs that would be produced the next season, these turtles would deposit 18 and 14 eggs, respectively. Hildebrand (1929: 30) reported that the annual egg production for the wild brood stock of Carolina terrapins (*M. t. terrapin* x *M. t. centrata*) averaged 14.4 eggs per female for a 12-year period. If it may be assumed that the annual reproductive capacity of the captive terrapins is representative of the natural populations of *M. t. terrapin* and *M. t. centrata*, then the gulf coast population may not differ in reproductive capacity.

The 11 juvenile females measured 13.3 to 16.0 cm. in plastron length. The smallest had the maximum ovocytes 3 mm. in diameter and the oviducts were not enlarged; the largest had ovocytes of 7 mm. in diameter and the oviducts enlarged. Hildebrand (1932: 561) stated that the female Carolina terrapins became sexually mature when they reached the length of 137 mm. but that one was mature at a length of 121 mm. There is indicated a substantial difference in the size at attainment of maturity in females between the gulf and east coast populations.

The males were 9.87 to 12.30 cm. in length; all were sexually mature and sexually active, with the vas deferens swollen with sperm. Hildebrand (1932: 561) observed that males of the Carolina terrapin developed the secondary sex characters at a plastron length of 80–90 mm.

Many of the turtles had distinct growth rings on the plastron. As these growth rings have been demonstrated to be acceptable indications of age and growth in other turtles (Cagle, 1950), it was assumed that the rings would provide a valid basis for age and growth determinations. The maximum length of each growth ring on the abdominal plate was measured with vernier calipers and this used to compute the plastron length at the time the ring was formed. Since the ring bordering the abdominal plate at hatching was still evident in 12 individuals (10 ♂♂, 2 ♀♀), their early growth history can be determined.

The calculated length of the 12 individuals at hatching was 1.80–3.57 cm.; end of 1st growing season, 3.03–6.11 cm.; end of 2nd, 2.44–8.67 cm.; end of 3rd, 7.54–10.73 cm. Only 10 of the turtles had rings representing the fourth season of growth; these were 9.11 to 11.55 cm. in plastron length. Six individuals with rings representing the fifth season indicated a plastron length of 10.25 to 11.75 cm. and two representing the sixth season a plastron length of 10.99 to 11.50 cm. Males thus may become

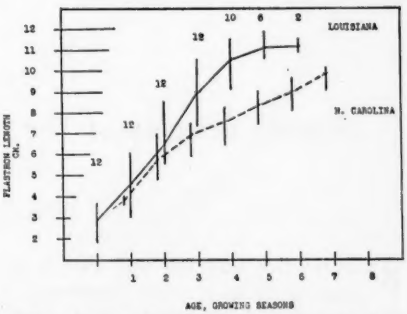


Fig. 1. A comparison of the growth of turtles from Louisiana and North Carolina. The vertical line indicates the range in plastron length and the figure above each line the number of individuals. The dotted line indicates the mean annual growth of 5 captive broods in North Carolina; the vertical lines indicate the range of the mean lengths in each brood.

mature before they complete the 3rd season of growth. Females do not become mature until after the 6th year.

A growth curve for the first six years was plotted from the calculated plastron lengths (Fig. 1). The characteristic rapid rate of growth, with a slowing at the time of attainment of sexual maturity, is evident. The mean annual growth for the first six years of 5 captive broods (1916—2, 1919, 1920, 1922) as reported by Hildebrand (1929, 1932) was plotted against this curve. The rate of growth for the first two seasons is similar but is much slower thereafter for the Carolina terrapin. Although the Louisiana males may attain the size at which they are mature during the 3rd season of growth the Carolina terrapins do not reach this size (p. l. of 8.0–9.0 cm.) until during their 5th season.

Unfotunately, there is no information on the rate of growth of either *M. t. terrapin* or *M. t. centrata* under natural conditions. The differences in rate of growth indicated here may be a difference in captive and wild individuals. If so, it appears that the growth potentiality of these turtles has never been fully exploited and that terrapin culture, particularly of the southern form, may be successful.

The intestinal contents of four individuals includes only the fragments of small clams and snails. Fecal material deposited in the sacks in which the turtles were transported was also composed solely of mollusk fragments.

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# Homing Behavior of The Painted Turtle and Muskturtle in a Lake

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RELATIVELY little has been done in attempting to learn about movements or migrations of fresh-water turtles. Cagle (1944) studied movements, homing behavior and migration in *Pseudemys scripta elegans*, *Chrysemys picta* spp. and *Terrapene carolina*. He found that individual aquatic turtles, removed from a particular region in a lake or stream, will usually return to that region when released; that aquatic turtles (except soft-shelled species) may move long distances overland; and that territoriality seems to be non-existent. He further noted that seasonal movements occur as wandering in the early spring and hunting for suitable hibernating quarters in the late fall. Pearse (1923) reported that of 166 painted turtles that were recaptured, 50 (30%) had travelled, while 116 (70%) had not. The average distance travelled was only 112 meters in an average of 5 months and 19 days. He states "Even after a year or two most of the tagged turtles were close to the place where they had been released. This shows that painted turtles are rather sedentary animals and, if their environment remains favorable, will remain in one locality for years." Risley (1932) noted that the number of muskturtles in shallow water in summer is apparently less than in the spring, probably due to increased activity and range, rather than migration from shallow to deeper water after the breeding season.

During the summer of 1949, while engaged in a fishing experiment for the Outboard Boating Club of America (Lagler, Hazzard, Hazen and Tompkins, 1950), I had the opportunity of conducting observations on the homing behavior of the central painted turtle (*Chrysemys picta marginata* Agassiz) and the muskturtle (*Sternotherus odoratus* (Latreille)). The locality was Fish Lake, Green Oak Township, Livingston county, Michigan, located about twelve miles north of Ann Arbor, Michigan. Fish Lake is a marl- and muck-bottomed lake of 36.5 acres with considerable encroaching shore line and a very abrupt drop-off along most of its perimeter.

Sixty-eight stations were marked off around the shore of the lake approximately 50 feet apart, except on a section of the east shore line where only two widely separated stations were located (Fig. 1). Fishing was done from 2 to 8 p.m. daily, June 20 to August 24, 1949 by three persons each in a separate boat. From June 20 to July 11 inclusive, only stations 19,

56 and 67 were fished, each station being fished by one person for the entire twenty-two days. From July 12 to August 2 inclusive, the same thing was done at stations 28, 46, and 68. From August 3 to August 24 inclusive each person drew randomly each day one of the sixty-eight stations to be fished. Each fishing station was at a point where the water depth was approximately 10 feet.

All fishing was done with cane poles or fly rods, using worms for bait, and all turtles were caught in this manner except for a few individuals unwary enough to be caught with the hands from the boat. The turtles apparently were never seriously injured by the hook, as it usually never penetrated their bony jaws and they were seldom hooked in the gullet. The turtles were measured to the nearest one-half inch, and were given a number which was painted on their backs with white enamel. Unfortunately some of the turtles started to shed their shields in August and thus lost part or all of their numbers, making it impossible, during the later period, to identify them. The white numbers had a distinct advantage over other methods of marking in that turtles could be identified in the water even when they showed no inclination to take the hook. All turtles caught were kept in the boat until the end of the day when they were released near the dock (Station 12). Records were kept of (1) original station of capture, (2) recapture station, and (3) station at which numbered turtles were seen but not caught, i.e., sight-record "recaptures" (Fig. 2).

In all, 98 painted turtles, averaging 4½ inches in length of carapace (range 2½ to 6 inches), and 50 muskturtles, averaging about 3¼ inches in length of carapace (range 2½ to 4 inches), were marked (Table I).

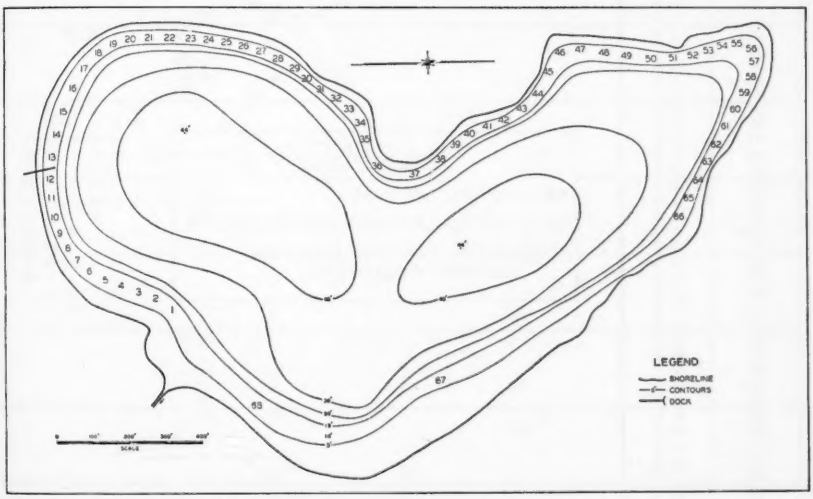



Fig. 1. Map of Fish Lake, Livingston County, Michigan showing location of 68 fishing stations. (All stations were located as close to the 10-foot contour line as possible.)

In comparing the number of times the painted turtles returned to their original capture stations with their size, it seems that the smaller turtles (from 2½ to 4 inches) averaged a greater number of round trips than the larger turtles (4½ to 6 inches). This can be shown as follows:

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Length of painted turtles: | 2.5 | 3.0 | 3.5 | 4.0 | 4.5 | 5.0 | 5.5 | 6.0 |
| Average number round trips: | 1.0 | 1.1 | 1.5 | 1.2 | 0.8 | 0.6 | 0.7 | 0.4 |

Evidently the larger turtles have a greater tendency not to return to their original capture station, but instead to wander around the lake. This can be further shown by the fact that 51 percent of the turtles from 2½ to 4 inches returned to their original capture site at least once, while only 36 percent of the 4½- to 6-inch

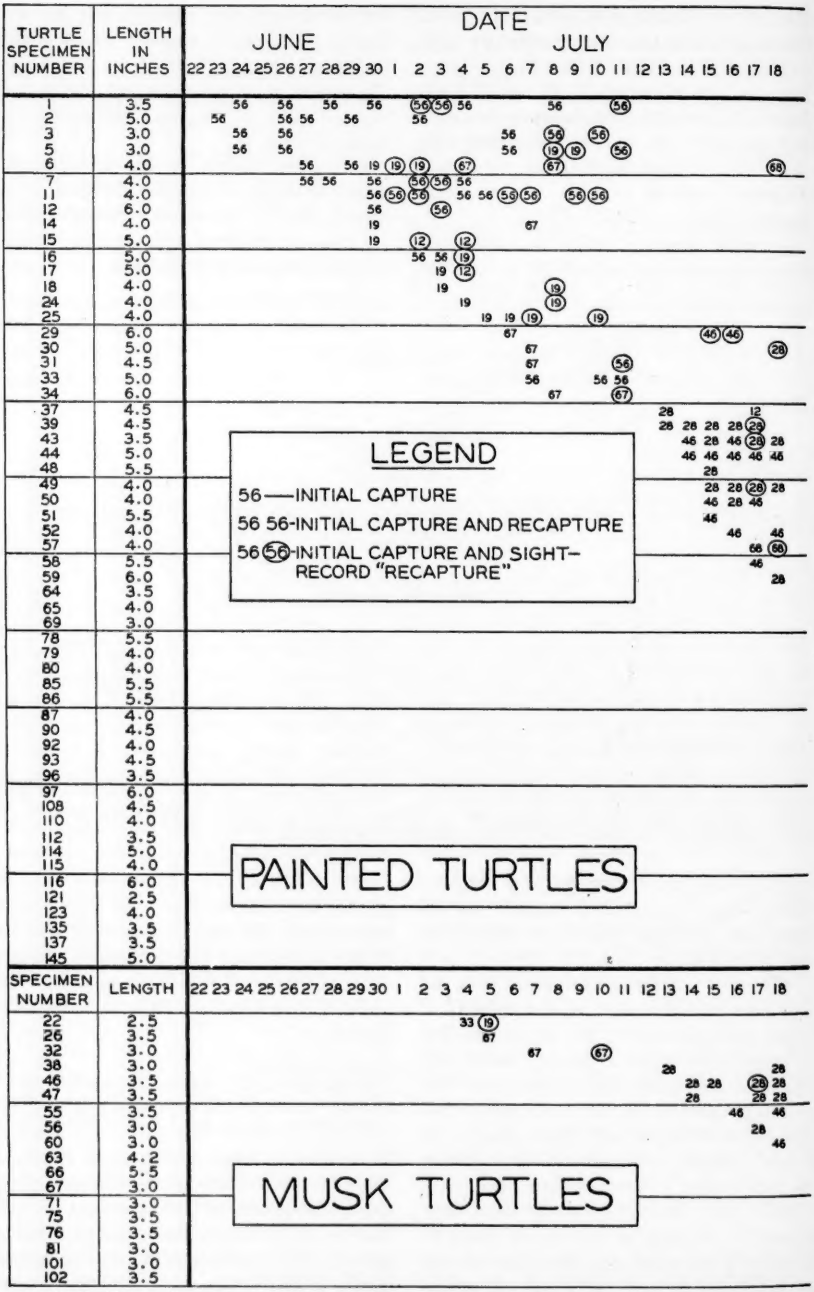
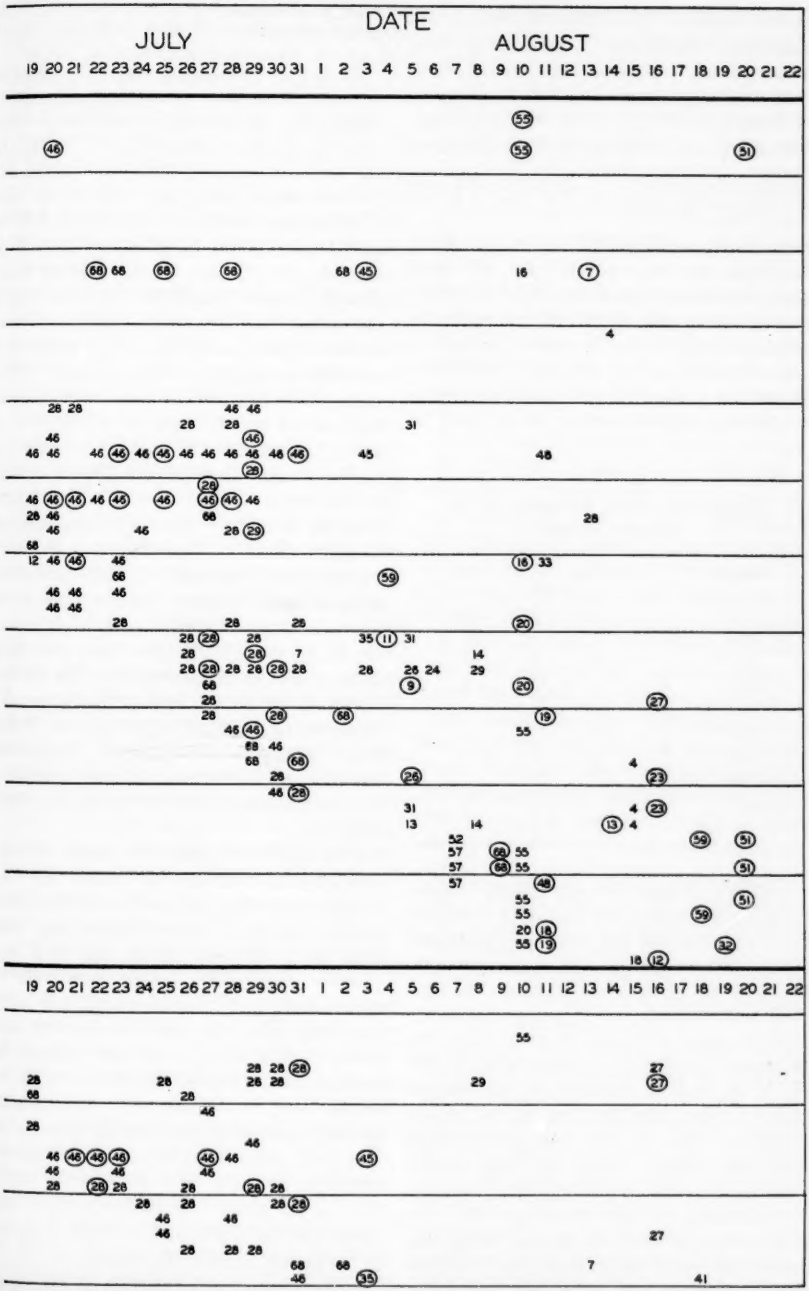

DATE
JUNE
JULY
22 23 24 25 26 27 28 29 30 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
TURTLE SPECIMEN NUMBER
LENGTH IN INCHES
LEGEND
56 —INITIAL CAPTURE
56 56-INITIAL CAPTURE AND RECAPTURE
56 (56)-INITIAL CAPTURE AND SIGHT-RECORD "RECAPTURE"
PAINTED TURTLES
SPECIMEN NUMBER
LENGTH
MUSK TURTLES

Fig. 2. Marking and recapture (including sight record) data for 57 painted turtles (upper portion of graph) and 18 muskturtles (lower) in Fish Lake, Livingston County, Michigan, summer of 1949. Collecting




stations numbered 1–68 (see Fig. 1). Station 12 (dock) was release point for all captured turtles. Circled numbers represent sight records, i.e. turtles seen but not captured.

turtles returned. While this difference is not statistically significant, it indicates a trend which possibly could have been proven statistically if a larger sample had been involved.

There is a different trend with the muskturtles, however, which can be shown as follows:

| Length of muskturtle: | 2.5 | 3.0 | 3.5 | 4.0 |
|---|---|---|---|---|
| Average number round trips: | 0.0 | 0.6 | 1.1 | 0.5 |

Here the small (2½-inch) turtles were never seen to return, while the medium- and large-size turtles returned more often. The differences are not statistically significant, but again the sample is small. Of the 50 muskturtles marked, none of the 2½-inch, 31 per cent of the 3-inch, 38 per cent of the 3½-inch, and 25 percent of the 4-inch group returned, as far as could be determined. Muskturtles are bottom-dwelling animals and therefore may have been at stations and not been noticed and recorded. The painted turtle, being more active, a more agile swimmer, and more apt to bask at the surface, is more likely to be noticed.

TABLE I

LENGTH-FREQUENCY DISTRIBUTION OF MARKED TURTLES

| Length | Painted | Musk |
|---|---|---|
| 2.5 | 1 | 4 |
| 3.0 | 7 | 25 |
| 3.5 | 10 | 17 |
| 4.0 | 33 | 4 |
| 4.5 | 14 | |
| 5.0 | 15 | |
| 5.5 | 11 | |
| 6.0 | 7 | |
| Total..... | 98 | 50 |

Of the painted turtles, 57 were never seen to return to their original station (or within 100 feet of it) while 41 returned to their original station at least once. However, during the last twenty-two days no two stations were fished twice and painted turtles had begun losing their shields; therefore the first forty-four days of the problem are more revealing in this part of the study. Of 60 turtles marked during this period, 24 never returned to their original station, while 36 returned at least once. For these 36 turtles, the returns were:

| Number of returns: | 1 | 2 | 3 | 4 | 5 | 6 | 7.....15 |
|---|---|---|---|---|---|---|---|
| Number of turtles: | 17 | 6 | 7 | 1 | 2 | 1 | 1.....1 |

As can be seen above, one turtle (No. 44, 5 inches in length) returned to its original station (No. 46, fished by the author) 15 times. This was during a period of only 29 days. In one seven-day stretch, during this period, No. 44 was caught every day. This means that after being released every evening at 8:15 PM at the dock, it had travelled to station 46 (a distance of 1,525 feet by the shortest route, directly across the lake) by 2 to 8 PM (nearly always by 2 PM) the next day. Thus in one week it had travelled a minimum of 1¾ miles. After skipping one day, No. 44 was captured 7 additional times and made 7 more trips from the dock in the next 10 days. After every one of these 7 releases at the dock, it was back at station 46 again the next day. Thus in 18 days it was captured 14 times and made 13 trips from the dock for a total minimum distance of 6,608 yards or 3¾ miles. It could have travelled along the shore between stations for a considerably greater distance. This turtle was taken again at station 45 three days after the 18-day period and again eight days later at station 48. Both stations are within 100 feet of the original station. During the 29 days, this turtle travelled a minimum of 4⅓ miles. Turtle No. 44 seemed to be exceptionally curious and unafraid and there may be some possibility that learning had an influence on its exceptional record.

In a total of 97 returns to original stations, painted turtles averaged 900 feet per day. This is certainly a minimum figure for several reasons partially explained above. Turtles may have gone along the edge of the lake and thus travelled considerably farther. Also these 97 returns include those whose returns were noted after long periods in which no observers were present. Again, many turtles had undoubtedly been at stations several days before being observed, even when observers were present. Basking spots were few and far between on Fish Lake and at least 95 per cent of the observations by sight were made while turtles were in the water. The maximum speed obtained was for turtles that returned to station 56 (2100 feet) in 18 to 23 hours.

Of the 50 muskturtles marked, 35 were never seen to return to their original stations. How-

ever, if turtles marked only in the first 44 days are considered, only 15 of 28 never returned. For the 13 turtles which returned, the number making various numbers of returns can be shown as follows:

| Number of returns: | 1 | 2 | 3 | 4.....8 |
|---|---|---|---|---|
| Number of turtles: | 4 | 4 | 3 | 1.....1 |

As with the painted turtles, one muskturtle made an exceptional record, considering their more secretive habits. This turtle (No. 46, 3½ inches in length) was captured 8 times and returned to station 28 (or within 50 feet of it) 8 times over a period of 34 days. Station 28 was at least 700 feet from the dock (across the lake), so this turtle travelled a minimum of 5,600 feet in 34 days. However, three times it returned the 700 foot distance in the 18-hour interval between release one evening and capture the next afternoon. An example of even more rapid travel is indicated by turtle No. 63 which returned to station 46 (at least 1,525 feet) in 18–23 hours. However the average for the 33 return trips made by 13 turtles was only a distance of slightly over 400 feet per day.

The question of whether or not turtles returned to their original stations by the most direct route across the lake is difficult to answer. It is my opinion that they follow the shoreline in either direction around the lake until they reach their home grounds. Turtles were never seen crossing the lake or surfacing in the center, even though a motorboat was operating on the lake for a considerable part of the time. Again, several times turtles were observed at a station between the dock and their original capture point and then observed a day or two later at their original station (turtles No. 5 and No. 23).

As opposed to those turtles with seemingly definite homing traits, other turtles seemed to wander about the lake, with no apparent home location. Turtles No. 17 and No. 59 were seen in nearly every part of the lake at various times. Other turtles stayed fairly close to their original sites for the entire summer (Nos. 5 and 96). Others would seem to spend longer periods at various locations in the lake (No. 6). The fact that these locations were occupied by fishermen may be an indication of the curiosity of turtles.

In all, 60 painted turtles were caught at the 6 fishing stations during the first 44 days. These turtles were seen a total of 188 times at the stations at which they were marked and 59 times elsewhere. After the turtles were marked they were seen 128 times at their home stations and 59 times elsewhere. Turtles marked in the latter part of the fishing had a lessened chance of being seen repeatedly at their home station. Disregarding this for the moment, if the turtles were distributed evenly among the stations after being marked, one would expect that they would have been seen eight times as often away from their home stations—of 9 periods fished (three, three-week periods and three men fishing) 8 are at stations away and one is at the home station—instead of a little less than half as often (59/128). Attempting to take account of the lessened exposure to being seen at their home stations, I calculate that the 60 painted turtles had 654 days of exposure to being seen at their home stations after marking and 6,600 days of exposure to being seen elsewhere (simply adding up for each turtle the number of days left after marking for it to be seen at its home station and the number of days left for it to be seen during each of the other 8 fishing periods and totalling for all 60 turtles). Now 6600/654 = 10.1. Thus assuming the marked turtles to be evenly distributed among all stations, they should have been seen more than 10 times as often away from their home stations as at them. Actually they were seen less than half as often away from their home stations. Therefore marked painted turtles were seen about 22 times ($10.1 \times 128/59$) as often at their home stations as they would be on the random distribution hypothesis. Separate analysis for each of the stations shows similar results; there is an excess of marked turtles seen at home stations over those seen elsewhere by ratios of 5:1 and up. These figures show a very highly significant difference between the painted turtle returns to original stations and random movements.

Similarly, with the muskturtles, 38 were caught at 6 stations in the first 44 days. These turtles were seen a total of 42 times at their home stations after marking (80 times counting marking capture) and only 7 times elsewhere. Thus, where one would expect after marking to see them 8 times as often away from their home stations, they were actually seen 6 times as often at their home stations. This is 48 times as often as they would be expected to be seen. Again, attempting to take account of the less-

ened exposure to being seen at their home stations, I calculate that the 38 muskturtles had 318 days of exposure to being seen at their home stations after marking and 3,660 days of exposure to being seen elsewhere. Thus assuming the marked muskturtles to be evenly distributed among all stations, they should have been seen more than 11 times (3660/318 = 11.5) as often away from their home stations as at them. Actually they were seen 6 times as often at their stations as away from them. Thus marked muskturtles were seen 69 times (11.5 × 42/7) as often at their home stations as they would be on the random distribution hypothesis. A very highly significant difference is thus also shown between muskturtle returns and random movements.

The phenomenon of returns from the dock to the home station for individual turtles is even more striking. As noted before, the champion, No. 44, returned to station 46 thirteen times in eighteen days. This would seem, on almost any theory, far from a coincidence. To make a rough estimate of the chance that a turtle moving at random would be seen 3 or more times back at his home station would require some assumptions to start with. Whether the ones made are at all in conformance with the facts would require additional knowledge of the mobility, wanderlust, etc. of turtles. However the assumption that a turtle is never present at two different fishing stations where observers were present, in the same day (and this occurrence is not reported), and that turtles travel at random from the dock, seem weaker than necessary. If we assume that the chance is no more than 1 in 10 that a turtle travelling at random would return to a particular station within two days, the chance that it would do this 3 consecutive times would be 1 in 1,000. When 148 turtles are involved the chance that a single individual would return 3 times in 6 days is about 1 in 7. Yet actually 6 painted turtles and 1 muskturtle did as well or better. Statistically this is extremely improbable if the movements were of a random nature. If we relax the time restrictions slightly, nearly twice as many turtles would be included. To this we must add that a turtle may be hindered in returning by disease, death or shock and that a turtle may be at or near a station but not observed.

It is therefore believed, from this experiment, that some painted and muskturtles show very definite indications of homing behavior, some individuals exhibiting it more strikingly than others. What reason lies behind this homing behavior is not so well shown. It may be entirely instinct or it may be a more or less steady travelling around the lake perimeter after release, until a recognized location is reached. In this study it was not possible to make enough observations on the turtles from the time of release to arrival at their home station, to indicate whether or not they always headed home along the closest shore line route. There is, of course, the possibility that learning or curiosity on the part of the turtles may have played a part in the experiment.

The author wishes to make grateful acknowledgment to William A. Tompkins, John Mulhall, Marvin O. Allum and Dudley W. Lester whose enthusiastic assistance in field work permitted the accumulation of records, and to the Outboard Boating Club of America whose research trust fund made this study possible. Sincere appreciation is also given to Dr. Karl F. Lagler, Chairman of the Department of Fisheries, School of Natural Resources, University of Michigan, for his encouragement and interest; to Dr. Cecil C. Craig, Director of the Statistical Research Laboratory of the University of Michigan, for his statistical assistance, and to Mr. William L. Cristanelli of the Institute for Fisheries Research for assistance in drafting the figures.

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# Fish Home Areas of Lake Myosotis, New York

HURST H. SHOEMAKER

IN the summer of 1946 the author conducted an inventory of abundance, lengths, weights, and ages of the fish of Lake Myosotis when on a research fellowship at the E. N. Huyck Preserve near Rensselaerville, Albany County, New York. The fishes were fin clipped and released in order to estimate their abundance by the Petersen method described by Ricker (1945). These fishes, taken from various parts of the lake, were carried by boat to the same dock (Fig. 1) for study and release. As certain recaptured individual bullheads could be recognized because of their unusual size, it became apparent that they were being taken repeatedly at the same netting station. Because of these observations and the suggestion by Dr. John Greeley that little was known about the homing movements of individual fishes in lakes, the study of home areas was incorporated with the other subjects mentioned above.

The fishes were trapped in three 1-inch mesh hoop (fyke) nets with wings, 2 throats, and 6 hoops. They were the style of net commonly used by commercial fishermen and were used with 50-foot leads. The nets were lifted once daily, at each of four stations, the catch placed in galvanized tubs, and rowed to the dock. Figure 1 shows the locations of dock "D" and stations designated as N.E., S.E., N.W., and S.W. Here they were sorted by species and retaken individuals were noted. After the routine examinations were made, the fish were marked by clipping of the fin chosen to indicate the corner of the lake from which they were taken. If taken from the northeast corner, the dorsal fin was clipped; if from the northwest, the top half of the caudal and right pelvic fins; if from the southwest, the right pelvic and bottom half of the caudal; and if from the southeast, the anal fin was clipped. If recaptured at a station other than the one of original capture, the fin indicating this second station was also clipped. The marked fish were then released at the dock, which was at variable distances from the collecting stations.

Because numerous pumpkinseeds (*Lepomis gibbosus*) were caught with hook and line at the dock, it was designated as station "D." Fish caught here were marked by clipping the spiny dorsal fin and were released at the point of capture.

The 90-acre artificial lake, supplied by two clear mountain streams which never went dry, was transparent to about 12 feet with the Secchi disc. The maximum depth along the old stream channel was about 20 feet but several acres at the north end had silted in to a depth of from 3 to 8 feet. The vegetation, chiefly cattail (*Typha*), *Anacharis canadensis*, and *Potamogeton crispus*, was very abundant at the north end and some was found around the entire edge except along the rocky dam at the south end.

Although movements of only two species are being reported in detail, there were indications that other species tended to return to the same stations where they were originally collected. As the number of individuals studied was so small, they are being omitted until further study can be made. The fishes showing the greatest tendency to return to home areas were the pumpkinseed, *Lepomis gibbosus* (Linnaeus), and the northern yellow bullhead, *Ameiurus n. natalis* (LeSueur).

*Pumpkinseed.*—In Figure 1 the arrows indicate that of the 142 pumpkinseeds captured at the northeast corner, transported to the dock, marked in the manner described above and released, there were 23 retakes in the northeast corner, three at the dock and one at the northwest corner. It illustrates that of the 190 captured at the northwest corner and released at the dock, there were 12 retakes at the northwest corner, four at the dock, and none at the other three stations. Of the 44 captured at the southwest corner and released at the dock, there were four retakes at the southwest corner, one at the northeast corner, one at the southeast corner, and none at the dock. Of 37 taken from the southeast corner to the dock, none was recaptured. This may have been due in part to the difficulty in setting nets in the southeast corner. The bottom was very hard and when there was any wind it was impossible to keep the net poles upright, so nets were seldom set at this station. Several small boys, who enthusiastically cooperated with the project,

caught 74 pumkinseeds on hook and line at the dock. Of these, 23 were recaptured at the dock and none went to any of the other four stations (Fig. 1).

Table I summarizes the returns for the pumpkinseed. By reading downward diagonally from the upper left to the lower right corner, one sees that 62 retakes occurred at the station of original capture. The 10 below and above this represent the strays.

*Yellow bullhead.*—At the northeast station, 53 of the 81 yellow bullheads captured there and released at the dock were retaken at the point of original capture. One of the 81 was recaptured at the southwest and one at the southeast corners but none at the northwest (Fig. 2). Of the 36 yellow bullheads marked for the northwest corner, seven retakes were from the same station and two had strayed to the northeast corner. If fishes move around the shore in getting to their original home areas, one might expect this to occur. Though only 19 yellow bullheads were marked from the southwest corner, seven retakes occurred at the same station and none wandered to the other three. The diagonal in Table II shows that 70 yellow bullheads were retaken at their original station with only four representing strays in this group.

*Other species.*—Though numerous brown bullheads (*Ameiurus nebulosus*) were taken, they were in such poor condition it is not surprising that only 14 were recaptured. Many were found dead in the nets and around the lake shore; some of these had been previously netted. Such die-offs of this species in Lake Myosotis had been reported in previous years and this one

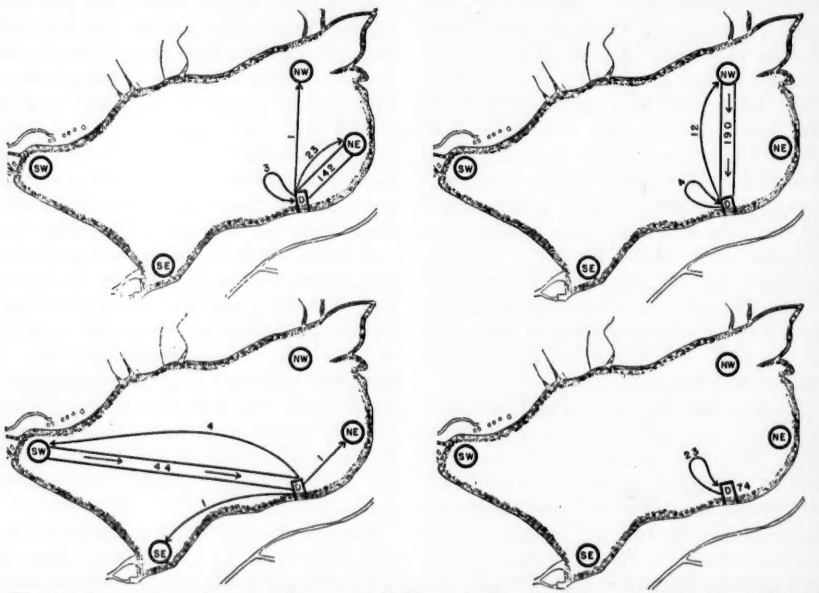


Fig. 1. Movements of *Lepomis gibbosus* in Lake Myosotis. Numbers by arrows represent numbers of marked fish recaptured at the stations indicated. Figure (see map at upper left) between double line (142) indicates number of fish originally caught at station NE.

TABLE I

NUMBERS OF *Lepomis gibbosus* MARKED AND RECAPTURED AT EACH STATION

| Place and number marked | Place and number retaken | | | | |
|---|---|---|---|---|---|
| | NW | SW | NE | SE | Davis dock |
| NW 190 | **12** | 0 | 0 | 0 | 4 |
| SW 44 | 0 | **4** | 1 | 1 | 0 |
| NE 142 | 1 | 0 | **23** | 0 | 3 |
| SE 37 | 0 | 0 | 0 | **0** | 0 |
| Davis dock 74 | 0 | 0 | 0 | 0 | **23** |

is therefore not to be attributed to their handling. Further study of this species will be required, because these sick fishes appeared to lose their orientation and behaved unnaturally, and because of the few individuals involved in the experiment. Also present in the lake were white suckers (*Catostomus commersoni*), white perch (*Morone americana*), golden shiners (*Notemigonus crysoleucas*), green sunfish (*Lepomis cyanellus*), smallmouth black bass (*Micropterus dolomieui*), and a few minnows too small to be taken in the nets used.

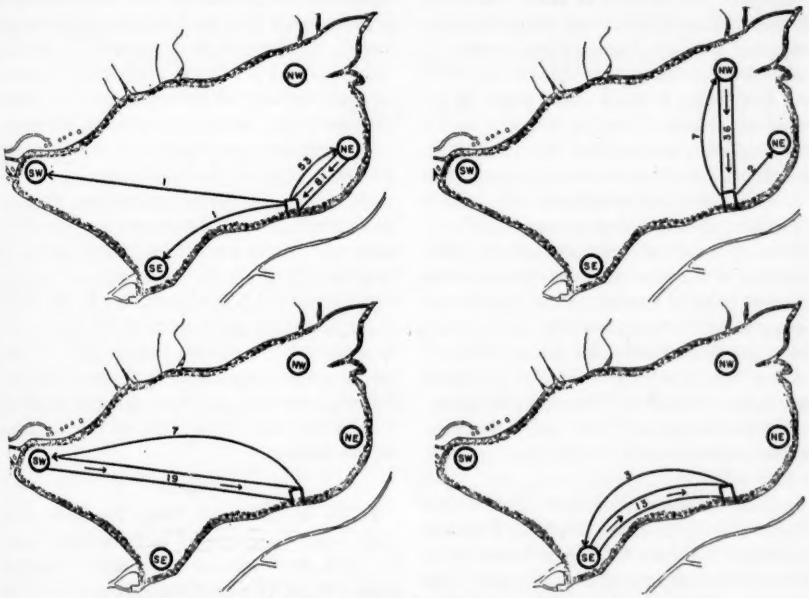


Fig. 2. Movements of *Ameiurus natalis* in Lake Myosotis. Legend as in Fig. 1

The Petersen method of estimating fish populations, based on the proportion of marked to unmarked individuals, assumes that they move at random (Ricker, 1945). Thompson (1933) showed that Illinois stream fishes traveled at velocities that were not consistent with the theory of strictly random motions. It is theoretically possible to correct for lack of randomness of movement by making the collections at numerous points over the entire area studied. However, as various species range over larger or smaller areas, the size of these areas may prove to be of considerable importance in making population estimates. Such precautions would appear to be unnecessary for other species, such as pike-perch (*Stizostedion vitreum*), which are reported to move at random.

We do not know how fishes return to their home areas. It is possible that they move at random until they get to familiar areas. Gerking (1950) and Schuck (1945) reported stream fishes returning after being moved from their original stations but, with only two directions to go, the problem is simplified. The literature on the home stream theory in salmon, though pertinent, is too extensive to review here.

Rodeheffer (1941, 1945) made studies of marked fish movements around brush piles in

TABLE II

NUMBERS OF *Ameiurus natalis* MARKED AND RECAPTURED AT EACH STATION

| Place and number marked | Place and number retaken | | | |
|---|---|---|---|---|
| | NW | SW | NE | SE |
| NW 36 | 7 | 0 | 2 | 0 |
| SW 19 | 0 | 7 | 0 | 0 |
| NE 81 | 0 | 1 | 53 | 1 |
| SE 13 | 0 | 0 | 0 | 3 |

Douglas Lake, Michigan. He noted that fish populations increased when these brush shelters were introduced into areas previously found to be practically barren of fish. He also found a great diurnal fluctuation in the fish population and reported that recaptures were made only in the near vicinity of original capture and release. Of the rock bass (*Ambloplites rupestris*) he captured and marked at Hook Point and released at East Point, about 10 percent were recaptured at Hook Point. In this connection Rodeheffer commented that "the return of fish from East Point to Hook Point might be regarded as evidence of homing behavior but no such conclusion is warranted by the facts at hand. Hook Point forms a natural trap and was a favorable and well-populated fish habitat even before the brush shelters were installed."

As all of the above recaptures in Lake Myosotis were of fish released some distance away from the point of capture, they demonstrate homing behavior. One of the two species best illustrating this behavior, the yellow bullhead, was not mentioned by Rodeheffer or others studying fish movements. The other, the pumpkinseed sunfish, he said "were so few that conclusions regarding their wanderings are not warranted."

Personal communication from Mr. Walter R. Crowe, Biologist of the Institute for Fisheries Research in Michigan, included information on the movements of several other species in Big Bear Lake, Otsego County, Michigan. In his study, fish captured at five widely separated stations were marked in a different manner for each station and released at the stations of original capture. Fifty-six percent of white suckers, 49 percent of largemouth black bass, 49 percent of smallmouth black bass, 48 percent of pumpkinseeds, 37 percent of bluegills, 57 percent of rock bass, and 50 percent of brown bullheads recovered were taken at the station of original capture and release. Crowe stated that the bluegill (*Lepomis macrochirus*) was "more inclined to move about than the other species" and that experience with this species on other lakes had been similar. This study strongly suggests a tendency in these species to stay in home areas. However, because of the possibility that more of them were re-caught at the original stations because of their closer proximity, it would appear inadvisable to state that home areas were conclusively demonstrated. Crowe stated that experiments to test homing were planned.

Our studies at Beaver Dam Lake in the summer of 1947 (unpublished) showed that only 55 percent of the bluegills retaken were at the station of original capture. But as only 66 percent of the black crappies (*Pomoxis nigromaculatus*) and 59 percent of the white crappies (*P. annularis*) were recaptured at the original station, the low return of these three species there appeared to indicate a possibility that the extreme turbidity of the water or some other physical factor, not present at Lake Myosotis, could have been responsible. Or the fact that different species were involved might be another explanation why these percentages were so much lower than the 86 percent for pumpkinseeds and the 95 percent for yellow bullheads in Lake Myosotis. Personal communications with Dr. Samuel S. Eddy and Dr. R. W. Eschmeyer regarding movements of pike-perch indicated that this species showed little if any tendency towards home areas. If environmental influences as well as species differences affect home areas, much more study will be required on this subject.

## Summary

Fishes in the 90-acre Lake Myosotis, New York, were demonstrated to have home areas to which they returned when moved to other areas. Of the 72 pumpkinseeds recaptured, 62 (or 86 percent) were taken at the station of original capture. Of the 74 yellow bullheads recaptured, 70 (or 95 percent) were taken at the original station. Some species of fishes, such as pike-perch, show no homing tendency while others show it in varying degrees. Not enough data are available for the same species from different lakes to show the effects of local conditions on homing. There is need for more information on fish movements because of its importance in estimating fish populations.

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# First Record of the Deepsea Fish *Dolichopteryx longipes* from the Pacific, with Notes on *Ophthalmopelton macropus*

MARION GREY

WHILE identifying some oceanic fishes taken in 1948 off Bermuda a need arose for specimens of the genus *Dolichopteryx* Brauer, none of which was included in our collection. Dr. William Beebe kindly offered us the loan of three specimens of *D. longipes* (Vaillant) from Bermuda and a hitherto unrecorded one from near the Galápagos Islands, apparently the first record of the genus from the Pacific Ocean.

The following descriptive notes on the Pacific specimen are published with Dr. Beebe's permission.

*Dolichopteryx longipes* (Vaillant)

No. 6342, Arcturus Oceanographic Expedition; Station 84, Net T-10; 1 mi. north of Narborough Island Galápagos Islands, June 9, 1925; depth 300 fathoms; standard length 63 mm.

DESCRIPTION.—D. 11, A. 9, P. 14, V. 10. Dorsal fin-fold extending from nape to caudal, interrupted only by dorsal and adipose dorsal; ventral fin-fold present between caudal and anal and between anal and vent; belly flattened from anal to below pectorals; ventrals situated at sides of flattened belly, turned outward, the upper 3 or 4 rays somewhat thicker and less flexible than the others; ventrals and pectorals pedunculate, ends of rays broken; body not compressed except behind anal.

PIGMENT.—A row of chromatophores along edge of lower jaw; somewhat behind this a row along lower side of head; a patch of chromatophores below and in front of eye and a band along top of snout centrally; a patch on sides of upper jaw; a sprinkling of chromatophores on bases and lower parts of rays of ventrals and pectorals, and on bases of dorsal and anal; one spot on each body myomere between vertical from pectorals and ventrals, below middle of body; posteriorly from above the ventrals a spot per myomere is also present above the middle of the body, increasing to two or three per myomere and gradually becoming more thickly distributed towards caudal; flattened portion of belly, excepting at edges and along a narrow central strip, showing silvery-brown through the thin transparent skin.

MEASUREMENTS.—The following measurements are given first in millimeters and then (in parentheses) in hundredths of the standard length (63 mm.): head 22.5 (35.7); snout to orbit 9 (14.3), snout to eye 10.5 (16.7); length of orbit 6 (9.54), length of eye at top 2 (3.18), height of eye nearly 3 (4.76); width of pupil and light organ 3 (4.76); postorbital (from orbit) 8.5 (13.5), postorbital (from eye) 10–10.5 (15.9–16.7); length of dark stripe on snout 7.5 (11.9); upper jaw 3 (4.76); snout to pectoral 20 (31.8), snout to ventral 40 (63.5), snout to dorsal 45.5 (72.3), snout to anal 49 (77.8), snout to vent 47 (74.6), snout to adipose 55 (87.4); end of dorsal to adipose 5 (7.94); vent to anal 2 (3.18); end of anal to base of caudal 12 (19.1); dorsal base 4.5 (7.15), anal base about 3.5 (5.55); length of pectoral including peduncle 9.5 (15.1), length of ventral including peduncle 11.5 (18.3); depth at eye 7 (11.1), depth at nape 7 (11.1), depth at pectoral about 6.5 (10.3), depth at ventral 4.5 (7.15); least depth of caudal peduncle 3.5 (5.5); width just before pectoral 5 (7.94), width just before ventral 4–4.5 (6.35–7.15), least width of caudal peduncle 1.5 (2.38), width of belly halfway between pectoral and ventral 5 (7.94).

Measurements in hundredths of the head

length: snout to orbit 40.0, snout to eye 46.6; orbit 26.7, length of eye at top 8.9, height of eye 13.3; width of pupil and light organ 13.3; postorbital (from orbit) 37.8, postorbital (from eye) 44.5–46.6; upper jaw 13.3.

Chapman (1942) stated that further research may show that the Dolichopterygidae are related to the group of fishes comprising the suborder Opisthoproctoidea (families Opisthoproctidae, Macropinnidae, Winteriidae, Xenophthalmichthyidae, Bathylagidae, Microstomidae and Argentinidae). It was his opinion that anatomical studies on some of the families are needed before an extensive definition of the suborder and the families contained in it can be undertaken. Since most of these fishes are extremely rare, any similarities that might have a bearing on their relationships to one another should be recorded, although no attempt is being made here to establish any such relationships, in accordance with Chapman's opinion.

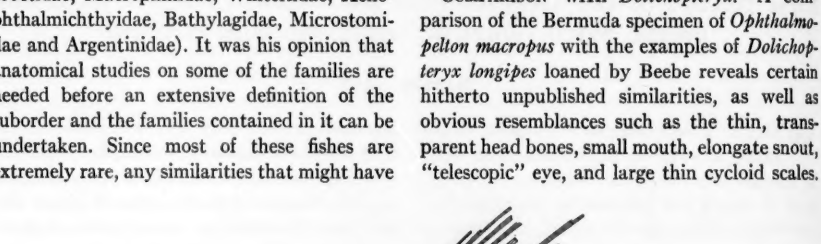


Fig. 1. *Ophthalmopelton macopus*, CNHM No. 49560, 94 mm. standard length. Drawn by Margaret Bradbury.

### *Ophthalmopelton macropus* Maul

Six years ago Maul (1946) described a new genus and species from Madeira that belongs to the group of fishes under consideration. A second specimen of this species (Fig. 1) was taken by the Bermuda Deep-sea Expedition of 1948 (conducted jointly by the Chicago Natural History Museum and the Bermuda Biological Station) in lat. 37° 02.2′ N., long. 64° 57′W., July 12, in an open net hauled in about 300 fathoms. Maul placed his new genus in the family Macropinnidae (Chapman 1939), stressing its relationship to *Macropinna* Chapman. Examination of the description and figure of *Rhynchohyalus natalensis* (Gilchrist and von Bonde) (1924), a species very similar to *O. macropus* Maul, indicates that the latter should rather be placed in the family Winteriidae as defined by Chapman (1942: 301). The general resemblance of larval specimens of *Macropinna* to *Ophthalmopelton* and *Rhynchohyalus* suggests a possible close relationship between the Macropinnidae and Winteriidae.

Comparison with *Dolichopteryx*.—A comparison of the Bermuda specimen of *Ophthalmopelton macropus* with the examples of *Dolichopteryx longipes* loaned by Beebe reveals certain hitherto unpublished similarities, as well as obvious resemblances such as the thin, transparent head bones, small mouth, elongate snout, "telescopic" eye, and large thin cycloid scales.

The presence of an adipose fin in a species of *Dolichopteryx* is a possible indication of its relationship to *Ophthalmopelton* and so, also, are the flattened belly, the curved ventral bases, and the differentiation of some of the ventral rays. A slender, delicate adipose dorsal fin is present in Beebe's largest Bermuda specimen[1] as well as in the Pacific specimen described above. In the two smaller examples (35.5 and 40 mm.) loaned by Beebe no adipose could be found, perhaps owing to their damaged condition. Although the larger Bermuda specimen is in very poor condition, as noted by Parr (1937: 35), the caudal peduncle is intact and the adipose fin undamaged.

In *Dolichopteryx* the ventral surface is flat-

[1] Beebe (1933: 70) stated that the standard length of this specimen is 85 mm. but Parr (1937: 35) measured it as at least 91–91.5 mm. and perhaps 95 mm. The specimen is now broken in two and no attempt has been made to measure it a third time.

tened from below the pectorals to the anal fin, in *Ophthalmopelton* from just behind the head to the anal fin. This condition has been confirmed in the type of *O. macropus* by Mr. Maul (*in litt.*) and is present in the largest Bermuda specimen of *D. longipes* as well as in the Pacific example. The damaged condition of the two smaller Bermuda specimens makes it impossible to determine the shape of the ventral surface but flattening of this region is probably general throughout the genus *Dolichopteryx*.

The ventral fins of both genera are situated at or just above the edges of the belly, and are thus rather widely separated; their bases are somewhat curved or elbowed. In *Ophthalmopelton* the two upper, or outer, ventral rays are lighter in color and somewhat thicker than the ten more flexible black rays. A similar differentiation of these rays is also evident, though rather vaguely so, in the two larger specimens of *D. longipes* at hand, and is described by Beebe in *D. binocularis*, which has three thick upper rays and six fine lower ones. Division of these rays is not evident in the two small Bermuda specimens.

A further external resemblance between *Dolichopteryx* and *Ophthalmopelton* is the presence in the latter genus of a large light organ (Fig. 1) on the side of the eye, directed obliquely downward, although the relationship of the light organ to the eye is perhaps more nearly like that in *Winteria* Brauer than it is in *Dolichopteryx*. Although the structure was strikingly visible in the freshly caught specimen of *Ophthalmopelton*, and was observed at the time by several members of the expedition and sketched by one of them, the light organ is now invisible, the side and front of the eye being covered by a deep black shield. Since preservation the organ has revolved downward, facing the floor of the orbit, and it is possible that in life the fish is capable of revealing or concealing it as the occasion demands. Maul did not mention such a structure in his type description of *O. macropus* but since the organ disappeared from view so surprisingly in our example, which is almost identical with the type in other respects, it seems highly probable that the type specimen also possesses it.

Exclusive of anatomical features, *Dolichopteryx* differs chiefly from *Opthalmopelton* in its more elongate form, relatively smaller eye, position of the light organ on the eyeball, and the more posterior positions of its vent and ventral fins.

MEASUREMENTS.—The following measurements were made on the Bermuda specimen of *O. macropus*, the numbers in parentheses representing hundredths of the standard length (94 mm.): length of head 40 (42.5); greatest depth 22 (23.4); greatest width 13 (13.8); length of snout to upper anterior edge of orbit 18 (19.2), length of snout to anterior edge of black shield below eye 16 (17.0); horizontal diameter of eye at top 9 (9.6), vertical diameter of eye 9 (9.6), greatest horizontal length of eye 11 (11.7); least depth of caudal peduncle 10 (10.6); tip of snout to pectoral base 37 (39.4), tip of snout to ventral 49 (52.2), tip of snout to dorsal origin 59 (62.8), tip of snout to anal origin 76 (81.0), tip of snout to vent 54 (57.5); vent to anal fin 21 (22.4), vent to caudal fin 41 (43.5); length of pectoral 15.5 (16.5), length of ventral 35 (37.2), length of caudal 18.5 (19.7); dorsal base 14 (14.9), anal base 8 (8.5).

The specimen is in rather poor condition. The left eye and probably some of the fragile head bones are missing, as the head sustained a certain amount of damage from contact with the net and from drying. The opercular and jaw bones seem to be largely intact but it has been impossible to determine the outlines of the other head bones, which are very thin and transparent. The mouth is terminal, small, similar to that of *Macropinna* Chapman; minute teeth are present in upper jaw; snout elongate, transparent and with the consistency of hard jelly in the freshly preserved specimen; flesh firm; scales fairly large, very thin, cycloid, striated, probably covering body in life but now lost except two on flattened belly just behind vent and three on right side beneath gill-cover, near pectoral fin; vent prominent, on a broad, low papilla placed on a level with the posterior end of ventral bases.

COLOR.—On fresh preservation, the color was whitish with some duskiness, especially on tail and along mid-line of body; mid-ventral and mid-dorsal lines quite black, the black area broadened around vent; caudal dusky at base, otherwise colorless; dorsal, anal, and pectorals dusky; the two outer ventral rays dusky, remainder of fin black; adipose dorsal black;

cheeks and opercles silvery, the latter with bluish reflections; snout entirely transparent except at tip where there is some duskiness that extends a short way backward on sides. The colors have changed very little but there is no longer any silver on the opercles, which are black due to the black lining of the gill-cavity showing through the transparent bones.

The specimen agrees with the excellent description of the type in all characters not mentioned above.

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# On the Utility of the Saw of the Sawfish

C. M. Breder, Jr.

THE relatively few mentions of the use which *Pristis* makes of its well armed rostrum mostly call attention to its utility as a defensive weapon. Of this there can be no doubt in the mind of anyone who has had to handle these essentially dangerous animals. Meek and Hildebrand (1923: 65) wrote, "The large saw-like rostrum probably is not used extensively as an offensive weapon, but it does constitute an effective defensive weapon, as the fish is able to strike from side to side with great force." Nichols (1929: 185) stated, "It is said that it disables small fish by striking from side to side with its peculiar weapon, and very probably also uses this implement to rake shelly creatures from the sand, if one may judge from indications of wear on the teeth of its saw, and the character of the teeth in its mouth, which are adapted to such food. When a sawfish is attacked, the saw becomes an efficient, dangerous weapon of defence." Norman and Fraser (1937: 62) discussed the matter more fully, among other things as follows, "The 'saw' may occasionally be used as a defensive weapon, but as a general rule its purpose is to obtain food, and this may be done in two different ways. The Saw-fish may grub about in the sand or mud, turning it over in its search for small fishes and other creatures lying buried there, or it may rise among a shoal of fishes swimming in the water, and, by striking rapidly from side to side, create havoc among them, leaving a number of stunned or dead victims to be devoured at leisure. On occasions it may even attack larger fishes, cutting large lumps of flesh from their bodies with the 'saw', but stories of its attacking whales are probably without foundation."

Irvine (1947: 97–98) wrote of *P. perotteti* as follows, evidently based on personal observation: "The 'saw' is used mainly for disturbing the small animals on which it feeds, but it is also used at times with strong side-strokes among a shoal of fishes, tearing off pieces of flesh which are afterwards devoured."

It is my purpose here to further discuss the use of the saw in connection with small fishes. Since an individual *Pristis pectinatus* Latham has been housed in one of the retaining pens at

*Upper: Pristis* "wigwagging" as its feeder approaches.
*Lower: Pristis* striking a floating fish and impaling it on the rostral denticles. The "wake" of the blade indicates nicely the length of arc struck by the fish.

*Photographs by F. G. Wood.*

the Lerner Marine Laboratory at Bimini, it has been possible to study in some detail the methods employed by the fish in this regard, which are not in complete accord with what has been current in the literature as exemplified by the preceding quotations. The fish in question is customarily fed small fish or pieces of larger fishes. If such a piece is on the bottom the fish merely swims over the food and evidently picks it up directly by its mouth much after the manner of the more thoroughly depressed skates. However, if a piece is slowly falling through the water or floating, the sawfish will swim up to meet it. When in an appropriate position it will strike sidewise at the food and neatly impale the object on one of its sawteeth. Then it promptly swims to the bottom and scrapes the food off against the bottom and swimming rapidly forward engulfs the food. This was witnessed many times by myself as well as by many other persons. The impalement was not merely a likely accident but surely a deliberate part of the behavior.

Such behavior amid a school of smaller fish would lead to the condition described by Norman and Fraser (1937), previously quoted, but is evidently a much more accurately controlled method of food getting than a mere random slashing about in water packed with closely schooling fish. Also the indications of wear on the teeth mentioned by Nichols (1929) would follow from the procedure herewith described whether the fish used the rostrum for "digging" or not.

Within three weeks after the preceding observations were made, the sawfish had become more accommodated to life in captivity and changed its behavior considerably. When the time arrived for the feeder to appear, the fish would swim slowly about at the surface, often in a vertical direction with about one-half of its "saw" protruding through the surface. This would be wigwagged back and forth in a manner that made various of the non-biological observers suppose it was beckoning to its keeper. When a fish was tossed to it, more often than not, it would lazily pass its saw over and about the fish with no effort at impalement, suggesting that it was merely investigating the offered food. Following this it would often simply swim over the dead fish and engulf it at the surface. Evidently in the intervening period it had learned that impalement was unnecessary and there was no danger of the fish swimming away. An hour's delay in feeding was all that was necessary to revive its original energetic attacks on food objects.

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# The Embryonic Origin of the Gas Bladder in the Centrarchid Fish *Lepomis macrochirus macrochirus*[1]

ARTHUR EDWARD DUWE

IN this study the bluegill was chosen because the Centrarchidae is a family of fishes in which the functional gas bladder has no pneumatic duct connection with the esophagus. This type of gas bladder in other fishes is generally attributed to arise as a dorsal diverticulum of the esophagus by way of a pneumatic duct which subsequently atrophies. However, whether the gas bladder arises in the bluegill as conventionally described in other groups, or in some other manner, can be established only by direct study. This investigation, suggested by Dr. John W. Price, was consequently undertaken to determine the actual mode of embryonic development of the gas bladder in *Lepomis m. macrochirus* Rafinesque, and the time during which such development occurs.

Embryos and postlarvae of the following periods of incubation were studied: 1 day (7 and 19 hours); 2 days (7 and 19 hours); 3 days (9 and 21 hours); 4 days (9 and 21 hours); 5 days (21 hours); 6 days (9½ and 21 hours); 7 days (9 hours); 8 days (9 hours); 9 days (9 hours); and a 14-mm postlarva. The material was kindly supplied by Dr. G. D. Morgan of Denison university.

Sectioning was done by the paraffin method and staining was done in Mallory's phosphotungstic acid hematoxylin. As critical sections of each embryonic series were located, they were marked and photomicrographs were made (Pls. I–II).

The first manifestation of the gas bladder in the bluegill was observed in the three-day 21-hour embryo. It appears in sagittal sections as a dorsal diverticulum of the esophageal region of the alimentary canal at the level of the third pair of body somites (Fig. 1). Transverse sections of this stage of development show the gut lying to the left of the midline of the embryo and the diverticulum coming off the right side of the gut (Fig. 2). The four-day 9-hour embryo shows the diverticulum pointing toward the ventral edge of the notochord (Fig. 3). Later stages of incubation show the gut in the middle of the embryo and the gas bladder developing dorsad to it, a positional shift presumably resulting from a progressive absorption of yolk.

At six days and nine and one-half hours of incubation the gas bladder shows a high state of development having an open pneumatic duct and a well-developed *rete mirabile* (Fig. 4). At eight days and nine hours the *rete mirabile* has decreased in comparative size and the pneumatic duct is in a state of incomplete atrophy (Fig. 5). By nine days and nine hours of incubation the pneumatic duct is no longer in evidence and the *rete mirabile* has become so reduced in size as to render its function doubtful (Fig. 6).

The 14-mm bluegill postlarva has a membranous gas bladder and a poorly developed *rete mirabile*. At this stage of development the gas bladder is in its definitive condition.

It is thus established that the bluegill develops a physoclistous type of gas bladder, which, for a brief period during its differentiation, is of the ancesteral physostomous type. Between the third and fifth day of embryonic development, bluegills possess an esophageal diverticulum at first directed medially and to the right from the esophagus which is displaced to the left of the embryo's center. This development is suggestive of the ancestral condition. Later this diverticulum assumes a dorsal position through the medio-ventrad rotation of the gut as yolk is absorbed. This diverticulum differentiates into a distal gas bladder and a proximal pneumatic duct, a condition comparable to that of adult physostomous fishes. Between the sixth and ninth days of development, bluegills possess a *rete mirabile*, a feature well developed and persistent in many physoclistous adult fishes. However, both the pneumatic duct and *rete mirabile* are transitory structures, undergoing complete and partial atrophy, respectively, after existing a few days. Thus the 14-mm bluegill is equipped, like the adult, with a single, thin-walled gas bladder, but devoid, by atrophy, of a pneumatic duct and retaining only a vestigial *rete mirabile*.

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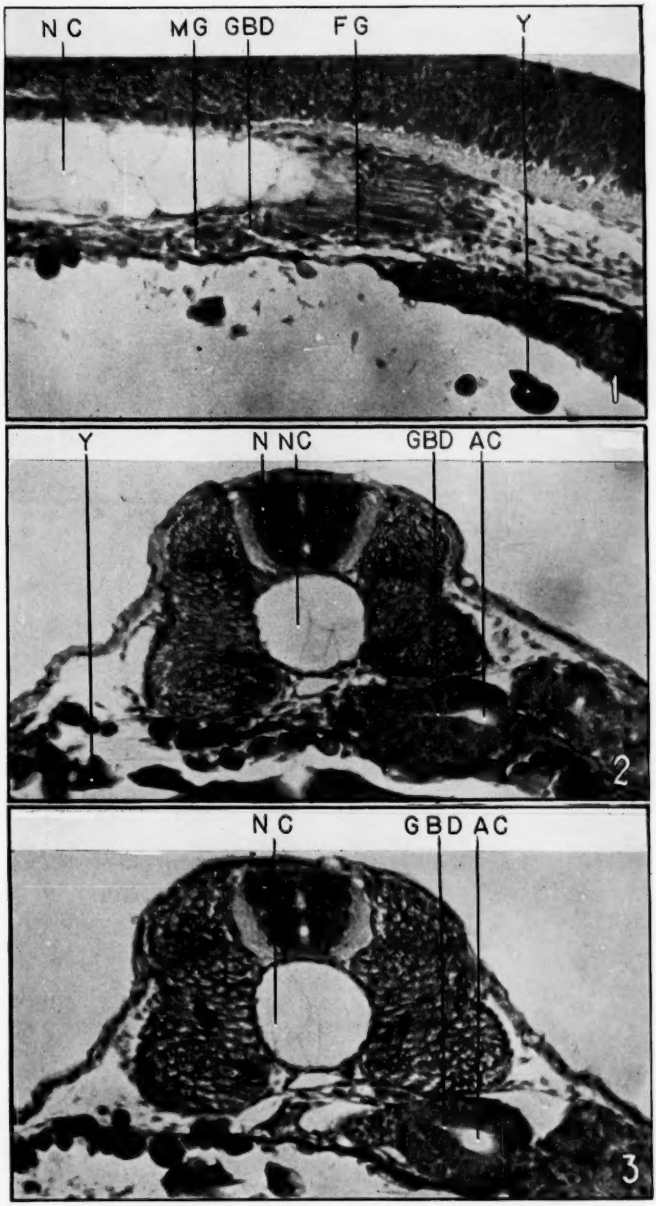
[1] Contribution from the Department of Zoology and Entomology, Ohio State University.



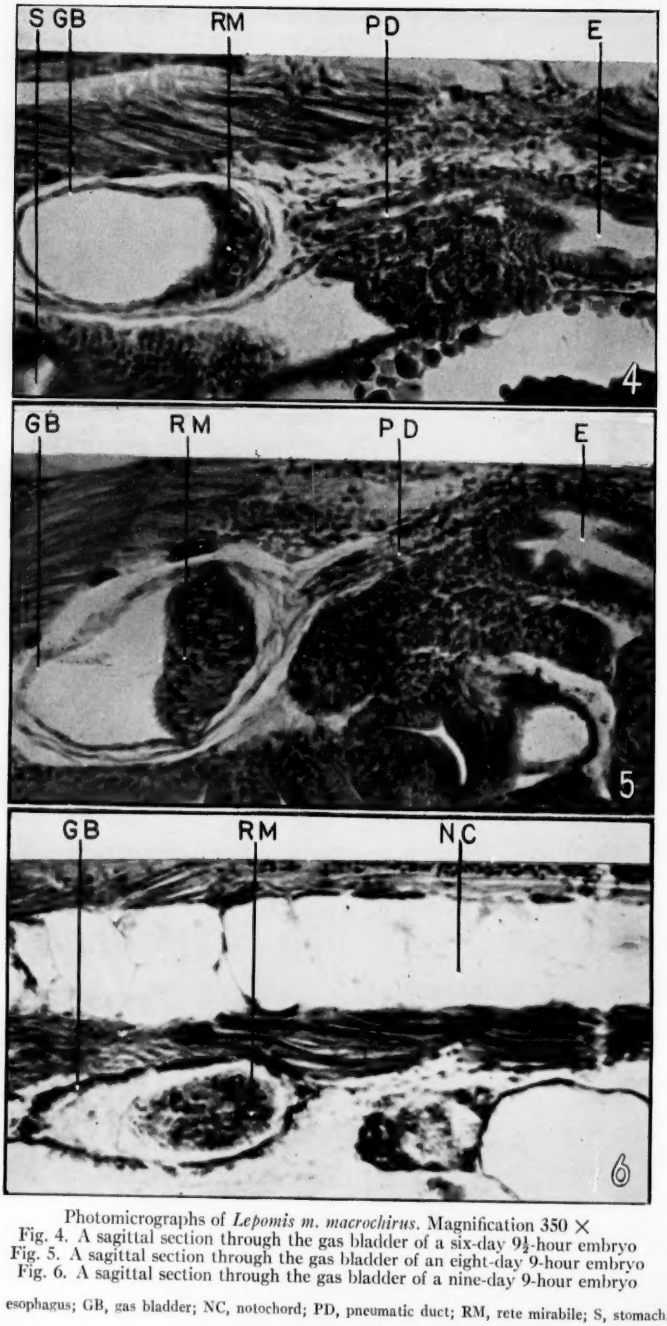

Photomicrographs of *Lepomis m. macrochirus*. Magnification 350 ×

Fig. 1. A sagittal section through the gas bladder diverticulum of a three-day 21-hour embryo

Fig. 2. A transverse section through the gas bladder diverticulum of a three-day 21-hour embryo

Fig. 3. A transverse section through the gas bladder diverticulum of a four-day 9-hour embryo

AC, alimentary canal; FG, foregut; GBD, gas bladder diverticulum; MG, midgut; N, nerve cord; NC, notochord; Y, yolk.




Photomicrographs of *Lepomis m. macrochirus*. Magnification 350 ×
Fig. 4. A sagittal section through the gas bladder of a six-day 9½-hour embryo
Fig. 5. A sagittal section through the gas bladder of an eight-day 9-hour embryo
Fig. 6. A sagittal section through the gas bladder of a nine-day 9-hour embryo

E, esophagus; GB, gas bladder; NC, notochord; PD, pneumatic duct; RM, rete mirabile; S, stomach.

# A New Lamprey, *Ichthyomyzon hubbsi,* from the Upper Tennessee River System

EDWARD C. RANEY

ABOUT fifteen years ago a nonparasitic lamprey was discovered in the mountain tributaries of the Tennessee River system of western North Carolina. More recently two series of breeding adults of the same species were taken in mountain streams of northeastern Georgia. The adults at hand number 23, and are adequate to demonstrate that it is a new species which is described below as

**Icthyomyzon hubbsi,** sp. nov.

Tennessee Brook Lamprey

Plate I

MATERIAL.—Holotype, Cornell University Fish Collection No. 20324, an adult male, 107.5 mm. in total length, taken in Nottely River, a tributary of Hiwassee River, Tennessee River System, 8 miles south-southeast of Blairsville on Georgia Highway Routes 19 and 129, Union County, Georgia, on April 10, 1947, by Robert D. Ross, Royal D. Suttkus and Raney. Five other specimens, C.U. No. 10985, 102.7 to 122.3 mm. total length, including 3 males and 2 females, were taken in the same collection and are designated as paratypes.

From the Little Tennessee River system the following are available and are designated as paratypes: C.U. No. 19532; a male 129.8 mm. and a female 125.1 mm. in total length, captured in a small tributary of the headwaters of Little Tennessee River at the north city limits of Dillard, on U. S. Highway 23, Rabun Co., Georgia, on March 25, 1951 by Richard H. Backus, Ronald W. Crawford, James N. Layne, Roland L. Wigley, C. Richard Robins, and Raney. University of Michigan Museum Zoology Fish Collection Nos. 136313 and 136314, 2 males and 12 females, 117.9 to 150.0 mm. long, taken in Oconaluftee River near Smokemont near Great Smoky Mts. National Park and Cherokee Indian Reservation line, Swain Co., North Carolina, on April 10 and 11, 1941 by Cowan Wikle; and U.M.M.Z. No. 141202, one male, 130.9 mm. long, from Raven Fork of Oconaluftee River above Ravensford, Swain Co., N. C., captured about June 1, 1943, by Cowan Wikle. Studied but not designated as paratypes was one ammocoete from the latter locality, and U.M.M.Z. No. 129556, 14 ammocoetes, 32 to 118 mm. long, from Oconaluftee River, about 1 mile south of Ravenswood, Great Smoky Mts. Nat. Park, Swain Co., N. C., collected by Carl L. Hubbs and family, on October 10, 1937. Also studied was U.M.M.Z. No. 136212, the remnants of one male and two females that were dead upon collection by Cowan Wikle, in Oconaluftee River, Cherokee Indian Reservation, N. C., on April 26, 1941. Also available in the University of Michigan Museum of Zoology are a large number of *Ichthyomyzon* ammocoetes, according to curator Reeve M. Bailey whose assistance in loaning specimens is much appreciated. These have not been used because of doubt as to their specific identification.

DIAGNOSIS.—A small, nonparasitic lamprey with a deep body, and low first dorsal and anal fins. Trunk myomeres 55–59 (mean 57.2 in adults). Snout short and buccal disk small. Dentition weak. Supraoral cusps normally 2; when a third cusp is present it is median in position and usually minute. Infraoral cusps 7 to 11 (mean 9.5). Circumoral teeth 20 to 27 (mean 22.3). Teeth in the anterior row 3–4 (mean 3.7). Teeth in the lateral rows 5 to 7 (mean 5.9). Bicuspid circumorals 5–10 (mean 7.7). Teeth only slightly, if at all, cornified. Transverse lingual lamina moderately bilobed, and lacks or has minute denticulations. Dorsal lateral line organs dark. Presumed to have been derived from the parasitic *I. bdellium.*

DESCRIPTION.—Counts and measurements were made using the methods described in detail by Hubbs and Trautman (1937: 27–40) in their excellent revision of the genus *Ichthyomyzon,* and are given in the same order so as to facilitate comparison with the known species of *Ichthyomyzon.* Measurements were made with dial calipers reading to one-tenth of a mm. See Vladykov (1949) for illustrations of structures mentioned herein. Measurements of the types are given in Table I and myomere and tooth counts are given in Table II. The myomere count of 11 ammocoetes from Oconaluftee

## TABLE I

MEASUREMENTS OF THE TWENTY-THREE ADULT *Ichthyomyzon hubbsi*

Total length in mm., and other measurements in thousandths of total length. For each character is given the range and mean (below). Number of specimens in parentheses after locality.

| Locality | Total length | Tail length | Body length | Eye length | Snout length | Disk length | Gill openings, length overall |
|---|---|---|---|---|---|---|---|
| Hiwassee R. Basin | | | | | | | |
| Ga., Nottely River | | | | | | | |
| Holotype | 107.5 | 276 | 86 | 11 | 67 | 46 | 98 |
| Paratypes* (5) | 102.7–122.3 | 290–306 | 77–95 | 13–15 | 56–67 | 43–51 | 91–103 |
| | 111.5 | 296 | 86 | 14 | 62 | 46 | 97 |
| Little Tennessee R. Basin, | | | | | | | |
| Ga., Trib. of Little Tennessee R. (2) | 125.1–129.8 | 281–301 | 78–81 | 13 | 60–62 | 41–42 | 105–106 |
| N. C., Oconaluftee R. near Smokemont (14) | 117.9–150.0 | 294–316 | 70–89 | 9–13 | 59–72 | 39–55 | 84–106 |
| | 133.5 | 305 | 78 | 11 | 63 | 46 | 98 |
| N. C., Raven Fork of Oconaluftee R. (1) | 130.9 | 301 | 80 | 11 | 74 | 49 | 103 |
| Range and mean, Little Tennessee R. Basin (17) | 117.9–150.0 | 281–316 | 70–89 | 9–13 | 59–72 | 39–55 | 84–106 |
| | 132.6 | 303 | 79 | 12 | 63 | 45 | 99 |
| Total range and mean (23) | 102.7–150.0 | 281–316 | 70–95 | 9–15 | 56–72 | 39–55 | 84–106 |
| | 127.1 | 301 | 80 | 12 | 63 | 46 | 98 |

* Mean includes holotype.

## TABLE II

MYOMERE AND TOOTH COUNTS OF TWENTY-THREE ADULT *Ichthyomyzon hubbsi*

For each character is given the range and mean (below).

| Locality | Myomeres | Supra-orals | Infra-orals | Circum-orals | Anterior rows | Lateral rows | Bicuspid circum-orals† |
|---|---|---|---|---|---|---|---|
| Hiwassee R. Basin | | | | | | | |
| Ga., Nottely R. | | | | | | | |
| Holotype | 58 | 2 | 10 | 23 | 4 | 6–6 | 8 |
| Paratypes* (5) | 55–58 | 2–3 | 7–10 | 20–23 | 4 | 6–7 | 5–8 |
| | 56.6 | 2.1 | 9.2 | 22 | 4 | 6.0 | 7.3 |
| Little Tennessee R. Basin | | | | | | | |
| Ga., trib. Little Tennessee R. (2) | 57–58 | 2 | 8–10 | 22 | 4 | 5–6 | 4–5 |
| N. C., Oconaluftee R. near Smokemont (14) | 56–59 | 2–3 | 9–11 | 21–27 | 3–4 | 5–7 | 7–10 |
| | 57.4 | 2.4 | 9.7 | 22.3 | 3.5 | 5.9 | 8.2 |
| N. C., Raven Fk. of Oconaluftee R. (1) | 57 | 2 | 10 | 25 | 3 | 6–7 | 9 |
| Range and mean, Little Tennessee R. Basin (17) | 56–59 | 2–3 | 9–11 | 21–27 | 3–4 | 5–7 | 6–10 |
| | 57.4 | 2.3 | 9.6 | 22.4 | 3.5 | 5.9 | 7.8 |
| Total range and mean (23) | 55–59 | 2–3 | 7–11 | 20–27 | 3–4 | 5–7 | 5–10 |
| | 57.2 | 2.26 | 9.52 | 22.3 | 3.7 | 5.9 | 7.7 |

† Occasionally trifid (4 teeth in 4 specimens).
* Mean includes holotype.

Above, *Ichthyomyzon hubbsi:* side view of holotype, an adult male, 107.5 mm. in total length. C. U. No. 20324.
Below, *Lampetra aepyptera:* side view of male, 107.5 mm. in total length. C. U. No. 17425. Taken on March 31, 1950, in a tributary of Oostanula River, 11.7 miles northeast of Rome, Alabama River System, Floyd County, Georgia.
Photographs by Douglass M. Payne.

River, which are probably this species, are 59(1), 58(2), 57(5), 56(3), mean 57.1, which is close to the mean for the adults (57.2).

Disk teeth weak, somewhat variable and stronger in the holotype than in most specimens from the same locality. Teeth shorter, more slender, and less well developed than in the related *I. greeleyi* and on the whole, slightly less degenerate than in *I. gagei*. In *hubbsi*, the teeth are best developed on the anterior half of the disk. Those on the posterior third of the disk are normally very poorly developed with 2 or 3 rows countable in the specimens in which the teeth are best developed. The anterior and lateral disk teeth in the holotype are long, thin, and are generally more rounded than the triangular teeth of *greeleyi*. The developed teeth point markedly posteriorly and a few are curved. Tooth cornification much weaker than in *greeleyi*. In most *hubbsi* there is little or no cornification of the supra and infraoral cusps and the teeth on the latter are usually small and difficult to count. The supraoral cusps are two in 17 out of 23 specimens. A third cusp was well developed in only one specimen, moderately developed in 2 others and very small in the 3 remaining specimens. The transverse lingual lamina is moderately bilobed and usually weakly cornified; the denticulations are very difficult to count. Four circumoral teeth (laterals) out of 177 are tricuspid. In the bi- (and tri-) cuspid circumorals the cusps arise independently from the base of the tooth.

The first dorsal fin is long and low (much lower than *greeleyi*) and the second dorsal is about one-half again as high. The height of the first dorsal fin does not reach the nostril when measured from the anterior margin of the eye. The anal fin is also very low and its greatest height, which is at a point immediately behind the anus, is less than or equals the length of eye. By contrast the first dorsal fin of *greeleyi* is much higher, and its greatest height is more than 2 times the length of the eye, and reaches far beyond the nostril when stepped off from the front margin of the eye. The second dorsal fin and the anal fin are also proportionately higher in *greeleyi*. In these fin characters *gagei* is like *greeleyi*, and differs from *hubbsi*.

In life *hubbsi* is moderately to weakly bicolored and is brownish gray above and greenish yellow, with small darker flecks, on the lower third of the body. It is more bicolored than *gagei* but somewhat less so than *greeleyi*. In most specimens of *hubbsi* the midline of the back before the dorsal fin is cream buff in contrast to the brownish gray area to either side. The blackish dorsal lateral line organs are prominent and serve to separate *hubbsi* from *fossor*, in which these organs are unpigmented. The lateral line organs on the ventral surface of the branchial region lack pigmentation. The fins are cream buff and suffused with small brownish flecks which are concentrated near the base of the caudal fin so as to make a marked contrast with the clear outer one-fourth to one-third of the caudal fin membrane.

SEXUAL DIMORPHISM.—The genital papilla is longer in the male. It is well developed, though not protruding, in the females available for study. The fleshy area in front of the genital papilla is somewhat more extensive in the female. The males are smaller on the average. The four males from Nottely River ranged from 102.7 to 117.5 mm. (mean 108.7) in total length while the two females were 112.1 and 122.3 mm. (mean 117.23). The mean length of 4 males from the Little Tennessee River System was less: 125.5 mm., range 117.9 to 130.9, compared with a mean of 137.0 mm., range 121.2 to 150.0, for 13 females. The situation is reversed in regard to disk and snout length. The snout length in four males from the Little Tennessee System averaged 69.5 (thousandths of standard length), range 62–74, and the 13 females averaged 61.5, range 58–67. Four males from Nottely River averaged 63.2, range 56–67, and the two females were 56 and 65, mean 60.5. The difference in length of disk is less pronounced. The males from Little Tennessee River average 49.0, range 41 to 55, the females average 45.8, range 39–49. The males from Nottely River average 46.7, range 43–51; the females average 45.5, range 45–46.

GEOGRAPHICAL VARIATION.—Too few specimens of each sex from the two drainages are available to draw any but tentative conclusions regarding intra-specific variation. However, if additional series show similar characters, the two populations seem to have differentiated at least on a racial level. The Nottely River population is smaller in total length, usually has fewer teeth and a generally more degenerate dentition, and has a larger eye. The 4 males

available from each locality do not overlap in size and the females only slightly so; 10 females from the Little Tennessee system are larger than either of the Nottely River females. Although the buccal disk is about the same size, the teeth are much smaller in the Nottely River population and there is a slight but consistently fewer number of myomeres, supraoral cusps, infraoral cusps, circumoral teeth and bicuspid circumorals. There is a reversal in number of anterior tooth rows (Tables I and II).

COMPARISONS AND RELATIONSHIPS.—Hubbs and Trautman (1937) recognized 6 species of *Ichthyomyzon*, 3 parasitic and 3 nonparasitic, and concluded that each of the 3 parasitic species had given rise to a nonparasitic species as follows:

| Parasitic species | Nonparasitic species |
|---|---|
| *I. unicuspis* Hubbs and Trautman | *I. fossor* Reighard and Cummins |
| *I. castaneus* Girard | *I. gagei* Hubbs and Trautman |
| *I. bdellium* (Jordan) | *I. greeleyi* Hubbs and Trautman |

It is postulated that *I. bdellium* also independently gave rise to a second dwarf derivative, namely *I. hubbsi*. A second possibility that both *hubbsi* and *greeleyi* may have evolved from a common nonparasitic ancestor which had earlier been derived from *bdellium*, is rejected on both morphological and geographic grounds as representing the least likely probability.

The close relationship with and probable derivation of *hubbsi* from *bdellium* is attested by the number of meristic characters in which *hubbsi* more closely resembles *bdellium* than it does the two other parasitic species. See Hubbs and Trautman (1937: 47), for counts and measurements of other *Ichthyomyzon* for the comparisons made below. It is close to or practically identical with *bdellium* in number of trunk myomeres, infraoral cusps, teeth in the circumoral row, teeth in the anterior row, and bicuspid circumorals. In the number of suproral cusps *hubbsi* is intermediate between *unicuspis* and *castaneus*. It differs trenchantly from *unicuspis* in the number of bicuspid circumorals. Also *hubbsi* stands apart from *castaneus* in the above mentioned characters and differs further in having the transverse lingual lamina moderately bilobed. There are fewer teeth in the lateral rows than all parasitic *Ichthyomyzon* but it is closest to *unicuspis* in this character. Like other nonparasitic *Ichthyomyzon* it differs from all the parasitic forms in its small size; shorter disk, eye, and snout; its degenerate dentition; and its life history (adult feeding stage omitted).

While it seems rather certain that *hubbsi* was derived from *bdellium*, the new species shows numerous differences when compared with *greeleyi*, which also is thought to have evolved from *bdellium* but perhaps at a later time and almost certainly at a more northerly locality, probably the Ohio River system in northwestern Pennsylvania. In tooth size and number *hubbsi* has diverged more from its parasitic ancestor. The relationship of *hubbsi* and *greeleyi* is attested by the reasonable closeness in body length, myomere count, the number of infraoral cusps, teeth in the circumoral row and anterior row, shape of the transverse lingual lamina, length of tail, and length over gill openings. The inner cusp of the mid-lateral bicuspid circumoral teeth is enlarged and triangular and approaches but does not quite attain the development found in *greeleyi*.

It differs from *greeleyi*, probably its closest relative, in normally having weaker tooth development with 2 (mean 2.26) supraoral cusps while *greeleyi* usually has 3 (mean 2.8); in fewer bicuspid circumorals (mean 7.7; 8.4 in *greeleyi*); fewer teeth in the lateral rows (mean 5.8; 7.2 in *greeleyi*); in greater body depth, and the difference here is marked (also greater than *fossor* and *gagei*); in having a shorter snout (between *fossor* and *gagei* with *greeleyi* having the longest); and in length of disk (occupying a similar position between *fossor* and *gagei* with *greeleyi* having the longest disk). It agrees with *greeleyi* and *fossor* and differs from *gagei* in having the transverse lingual lamina moderately curved. However denticulations on this lamina are absent or very poorly developed in *hubbsi* in contrast to the long slender ones present in *greeleyi*. It differs trenchantly from *greeleyi* in having lower dorsal and anal fins, as has been pointed

out above. It differs from *fossor* in possessing dark, dorsal lateral-line organs.

RANGE, HABITAT, AND ECOLOGY.—Apparently limited in distribution to the upper Tennessee River system where it has been obtained at altitudes above 1800 feet. Although now known only with certainty from northeastern Georgia and western North Carolina it probably also occurs in the same drainage in eastern Tennessee. Judging from the two localities at which the writer has taken it, adults prefer small headwater tributaries (tributary of Little Tennessee River) or medium sized mountain streams (Nottely River). At the former locality the water was white and clear; the flow was estimated to be 2 to 5 c.f.s.; the bottom was sand and fine gravel and lacked aquatic vegetation; and the depth was up to 1½ feet with short riffles and shallow pools which varied in width from 3 to 10 feet. The stream flowed through a pasture. The water temperature was 50° F., the air 61° F. at 6 P.M., on March 25, 1951, when one adult was taken in a riffle and the other was found lying quietly near shore. Six other fishes, *Hypentelium nigricans*, *Semotilus a. atromaculatus*, *Notropis coccogenis*, *Campostoma a. anomalum*, *Clinostomus* sp. and *Cottus carolinae* were taken in goodly numbers. The latter was abundant and 57 specimens were captured. Three yellow egg masses were found under one stone only 5 inches in diameter. Imminent darkness and an irate landowner prevented a thorough search of the locality, but this should be a good place to study the spawning habits of *hubbsi*. The nearby main stream, Little Tennessee River, is contaminated somewhat by domestic wastes from Dillard.

Nottely River was high from spring rains when seined on April 10, 1947. The water and air temperature were 54° F. at 5 P.M. It falls rapidly from its source in the mountain area immediately to the south, and has a large fish fauna. The water was white, slightly turbid, and was flowing at approximately 400 c.f.s. The riffles were long and about 2½ feet deep where *hubbsi* was taken. The deeper pools were over 5 feet and the width averaged 40 feet. The bottom was rubble and gravel with a small amount of sand and with some filamentous algae in the riffles. Other fishes were common and the species numbered 17 as follows: *Catostomus c. commersoni*, *Hypentelium nigricans*, *Moxostoma erythrurum*, *Semotilus a. atromaculatus*, *Hybopsis a. amblops*, *Hybopsis watauga*, *Rhinichthys cataractae*, *Notropis coccogenis*, *Notropis leuciodus*, *Notropis galacturus*, *Notropis spectrunculus*, *Campostoma a. anomalum*, *Hadropterus evides*, *Etheostoma maculatum*, *Etheostoma zonale*, *Etheostoma blennioides newmani*, and *Cottus carolinae*. The 6 *hubbsi* were probably a spawning group and were taken near the head of a moderately fast riffle. One or at most two specimens were picked up in a ten foot seine with ¼ inch mesh at the same spot as we worked downstream numerous times. The slight turbidity at a depth of 2 feet and the surface ripple prevented observation of the bottom. The fine collection of mature adults taken by Cowan Wikle on April 10–11 in Oconaluftee River near Smokemont were probably also a spawning group. The eggs were enlarged and apparently ripe in each of the females. It probably spawns somewhat later than the more southerly *gagei* (a nesting group was found in Russel County, Alabama on March 24, 1948; water 59° F.) but earlier, and probably at a lower water temperature, than either *greeleyi* or *fossor*. The former has been observed spawning in western Pennsylvania (Raney, 1939: 111) from May 19 to 26, when the water was 66° F., and *fossor* has been observed nesting in southern Michigan by Reighard and Cummins (1916: 7–10) on May 23 to 27, at a water temperature of 68° to 71.6° F. and by Hankinson (1932: 420) from May 10 to 13, at a water temperature of 71.6° F. Vladykov (1949: 43) reported that *fossor* spawns in late May in Quebec. Greeley (1930: 73) found *unicuspis* nesting as late as June 18, in a tributary of Lake Champlain, northern New York, when the water was 72° F.

LIFE HISTORY.—The new species is nonparasitic, judging from its small size, small buccal disk, and weak dentition. The collection of 14 larvae of what are presumed to be this species was made from a soft mixture of sand, mud and leaves by Carl L. Hubbs and family on October 10, 1937, in Oconaluftee River, about 1 mile south of Ravenswood, Swain Co., N. C. The current was sluggish, the water was up to 10 inches in depth, and the stream width was about 75 feet. Future study will probably reveal differences in proportional measurements and color of the ammocoetes of *hubbsi* and *bdellium* when adequate material of each is available.

This species is named for the distinguished ichthyologist, Carl L. Hubbs, Scripps Institution of Oceanography, La Jolla, California, who has contributed much to our knowledge of North American lampreys, in appreciation of the encouragement given the writer in his studies of fishes. He recognized the form herein named as new and collected some of the material as noted above. The common name, Tennessee brook lamprey, is deemed appropriate since it seems certain that it will be found to be a common form in the small headwater streams of the Tennessee River system.

Recent field work in Alabama has revealed *I. gagei* at several localities. In view of the scarcity of information on this species the following records are given: C.U. No. 13982: Thirteen adults were captured in a tributary of Uchee Creek of the Chatahoochie River System, 3.1 miles east of Marvyn on Alabama Highway 80, Russel County, Alabama, on March 24, 1948, by Suttkus and Raney. Included were 8 males, 90 to 98 mm. (mean 94) in total length and 5 females 108 to 115 mm. (mean 112.5) long. The fins were cream buff, the upper sides grayish brown fading to cream buff below and with pronounced dark, dorsal lateral-line organs on the upper sides. All were members of a spawning group taken over a fine gravel bottom at a depth of 2 feet in a moderately swift riffle about 10 feet wide. The water temperature was 59° F., the air 75° F., at 11 A.M. C. U. No. 14029: Three large ammocoetes, taken in a tributary of Conecuh River, 8.2 miles west of Troy, on Alabama Highway routes 10 and 29, Pike County, Alabama, on March 24, 1948, by Suttkus and Raney. They were kicked out of the sand bottom of a very small woodland stream. C. U. No. 17660: A male, 105 mm. and a female 109 mm., seined in Omussee Creek, a tributary of Chatahoochee River, 5.8 miles northeast of Dotham, on Alabama Highway 241, Huston County, Alabama, on March 28, 1950, by Backus, Suttkus, Robins, and Raney. They were taken in a riffle of a small, turbid Piedmont type stream. The water temperature was 65° F., the air 71° F., at 10 A.M. C. U. No. 18231: An adult female, 123.5 mm. long, from McIlray Creek, a tributary of the Chatahoochie River, 2.2 miles west of Fort Gaines, Georgia, in Henry County, Alabama, on March 28, 1950, by Backus, Suttkus, Robins and Raney. It was taken in a riffle of a medium-sized, shallow stream, falling rapidly through a deep rocky gorge. The bottom was of bedrock, boulders and sand. The water temperature was 68° F., the air 78° F., at 3:20 P.M.

If the available specimens are a representative sample, the female attains a larger size in *gagei*. The 9 males range from 90–105 mm. (mean 95.2) total length, and the 7 females range from 108 to 123.5 mm. (mean 113.2).

Some east to west variation in size in *gagei* is indicated by the scant available data, and the largest specimens so far recorded are found in the western part of the range as now delimited. Unfortunately the sex is not given for specimens reported in the literature. However, the adults reported above plus the single specimen from Alabama recorded by Hubbs and Trautman (1937: 84), range, in 17 specimens, from 90 to 126 mm. (mean 104.5) in total length, and the 10 Louisiana specimens reported by Hubbs and Trautman (1937: 84) range from 99 to 113 mm. (mean 105.3). The western specimens, although inadequate in number, average longer. Oklahoma specimens reported by Hubbs and Trautman (1937: 84) measure 105 and 144 mm.; by Bailey (1947: 146) 150 mm., and for Texas 109.5 mm.; and 166 mm. by Knapp (1951: 87) for Texas. The mean for 5 Oklahoma and Texas specimens is 134.9 mm. If additional specimens do not affect these results substantially, *gagei* has both the smallest (Alabama and Louisiana) and largest (Texas and Oklahoma) populations of nonparasitic *Ichthyomyzon*. The mean length as given by Hubbs and Trautman (1937: 70) for *fossor* (65 specimens) is 119 mm., and for *greeleyi* (109 specimens) 128 mm. The mean of 23 specimens of *hubbsi* is 127.1 mm.

Of interest is the discovery in the Alabama River system, Georgia, of what may prove to be a new subspecies of the eastern brook lamprey, *Lampetra aepyptera* (Abbott). This abberant, nonparasitic lamprey has been known heretofore from the upper Ohio River system (Creaser and Hubbs, 1922: 8) to the Wabash River system, Indiana (Creaser, 1939: 169) and on the Atlantic coast from the Potomac River to the Neuse River system (Raney, 1941: 318). Its presence hundreds of miles away from the above localities with several intervening river systems again points up the necessity for continued ichthyological exploration, especially in

early spring when many lampreys spawn, and indicates that *Lampetra aepyptera* is probably a widespread form. Only a single specimen, C. U. No. 17425, a male 107.5 mm. in total length, was taken in a tributary of Oostanula River, 11.7 miles northeast of Rome, Georgia Highway Route 53, Floyd County, Georgia, on March 31, 1950, by Backus, Suttkus, Robins and Raney. The stream was small, clear, of alternating pools and riffles, from 5 to 10 feet wide, and up to 3 feet in depth. The bottom was rubble, gravel and sand. The water and air were 56° F. at 12 noon (after a very cold night). Unfortunately the specimen has shrunken badly in preservation but the general appearance is preserved in the accompanying illustration (Plate I), photographed shortly after capture. It has only 54 trunk myomeres and is on the lower extreme of the range (54 to 60 according to Creaser and Hubbs, 1922: 8). There are no teeth on the disk other than an extremely weak marginal row, with another irregular subparallel row of very small teeth on the anterior disk only. No laterals are present such as are found in northern specimens (see Creaser and Hubbs, 1922: pl. 1). The supraoral cusp has two large, widely separated lobes which are toothless. The infraoral cusp is very long, has 6 marked crenulations, but lacks teeth. The transverse lingual lamina is slightly curved and toothless. The anterior lingual lamina is also toothless.

Some of the ichthyological explorations on which this new species was taken were made possible by grants from the Faculty Research Grants Committee, Cornell University, and by the cooperation of the several Cornell graduate students in ichthyology mentioned herein whose assistance is gratefully acknowledged.

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# Nomenclature of the Channel Catfish and the Burbot of North America

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The presently accepted name of the channel catfish of the Great Lakes is *Ictalurus lacustris* (Walbaum). Walbaum's (1792) description of *Gadus lacustris* was based on Pennant's (1784) account of a fish from the Hudson Bay region, which Pennant called "mathemeg" or "land cod." Richardson (1836) interpreted Pennant's "mathemeg" to be the same fish as his own *Pimelodus borealis* (which from its description was a channel catfish). Jordan and Gilbert (1883) and later writers have accepted this interpretation. It appears almost certain, however, that Pennant's "mathemeg" could not have been a channel catfish, but was

a large burbot. Consequently the name for the channel catfish should again become *Ictalurus punctatus* (Rafinesque) and the Hudson Bay form of the burbot should be known as *Lota lota lacustris* (Walbaum).

The earliest reference bearing on the identity of the "mathemeg" appears to be an article by Forster (1773) which was based on a letter to Thomas Pennant and deals with "a choice collection of skins of quadrupeds, many fine birds, and some fish," presented by the Hudson's Bay Company and "collected by their servants at the several ports in Hudson's Bay." Forster's account will be quoted at some length because several details are significant in the interpretation of Pennant's writings.

> The second of the Hudson's Bay fish, is called, by the wild natives of that country, Marthy, and is nothing else than our common Burbot, *Gadus Lota*, Linn. only vastly superior in size. The descriptions you have given of this fish, in the British Zoology, is entirely corresponding with this specimen, so that it would be superfluous to presume to make any additions to it. I must, however, observe, that, after a most minute examination, I could find no more than six branchiostegous rays in the two specimens from Hudson's Bay, of which you mention seven in the English Burbot, and Artedi as many in his specimens. This great naturalist seems likewise to be right, when he observes that the *cirri*, or beards on the end of the nose, are the valves to one of the nostrils; for I found that these beards, on their underside, opened into a hole, corresponding with the lower nostril. Mr. Andrew Graham, the collector of the Natural History specimens at Severn River in Hudson's Bay, observes, that these fish swim close to the ground, and are extremely voracious; for he represents them as not content with devouring every fish they can overcome, but likewise feeding on putrefying deer, or other carrion that comes their way; even stones are sometimes swallowed to satisfy their indefatigable appetite, of which Mr. Graham was himself a witness, having taken a stone of a pound weight out of the stomach of this fish. The pike is often obliged to fall a victim, together with the trout, *Tickomeg*, and others, to this rapacious fish. After sunset, it is caught by a night-hook. It does not masticate its food before deglutition. Its roe and liver are reckoned a delicacy, when fresh caught; but they turn rancid and oily in a few days, though kept frozen solid all the time. At Hudson's Bay this fish is thought to be dry and insipid; its weight is from one to eight pounds.

The above account indicates the original source of some of Pennant's information. Note also the native names: *Marthy* for the burbot, and *Tickomeg* for the whitefish; and the description of the *cirri*, which he calls "beards."

Pennant's (1784) account contains several sections pertinent to the identity of the "mathemeg". In the "Introduction" to his "Arctic Zoology," in his section on Hudson's Bay, he wrote (Vol. I: CXCI):

> The *Gadus Lota*, or Burbot, Br. Zool. ii. N° 86, is common in the rivers, and is caught with hooks after nine o'clock at night. It is here called *Marthy:* grows to the weight of eight pounds; is so voracious as to feed even on the tyrant Pike; will devour dead Deer, or any carrion, and even swallow stones to fill its stomach: one of a pound weight has been taken out of a fish of this species. It spawns about February 8th, and is unhappily most prolific. Mr. Hutchins counted, in a single fish, 671,248 ova.

Note that most of this description is "second-hand," from Forster (1773). Pennant has changed Forster's "After sunset, it is caught by a night-hook" to "it is caught with hooks after nine o'clock at night."

Immediately following the above account of *Gadus Lota* is this description:

> Allied to this is the *Mathemeg* of the natives, the Land Cod of the *English*, a fish abundant in the northern lakes; it grows to the length of three feet, and the weight of twelve pounds: has three beards on the lower jaw; the middlemost the longest: the back is brownish: the belly grey.

In Vol. II (1785) of the "Arctic Zoology" is a section entitled: "Supplement to the Introduction to the Arctic Zoology." On page 115 of this is listed:

> *Br. Zool.* iii No.—Gadus lota, *Lin.* 93. Burbot.
> Inhabits Hudson's Bay. See Introd. cxci. Place.
> Introd. cxci. 94. Mathemeg.
> Inhabits the lakes of Hudson's Bay. Place.

On page 137 of this supplement is the following significant item:

> Silurus Felis, Lin. 503. 160. Pelis.
> S. With four beards on the lower lip: above the mouth, one on each side: back blueish: ventral and anal fins red: tail bifid.
> Inhabits Carolina.—Doctor Garden. Place.

Also on page 137 Pennant described at some length "S. catus, Lin.," including such items as "With four short beards on the lower jaw, and a very long one issuing from under each eye: . . . the second dorsal fin without rays, and fat: tail forked and red . . . Grows to the length of two feet."

It seems clear that Pennant's "mathemeg" could not have been a channel catfish, which is not allied to the burbot. From his descriptions on page 137 it is clear that Pennant was

familiar with that fish. In his supplement he classed his "mathemeg" with the "jugular" fishes; his "Pelis" with the "abdominal" fishes. He associated his "mathemeg" with *Gadus lota* in both his references.

The channel catfish is not "abundant in the northern lakes" nor does it "inhabit the lakes of Hudson's Bay." In Ontario there are no records of the channel catfish north of the north end of Lake Huron; in Manitoba (Hinks, 1943) there are no records north of the north end of Lake Winnipeg; in Saskatchewan the only known record appears to be Richardson's old record from Pine Island Lake (now Cumberland Lake) at latitude 54° near the Manitoba border. In short, there are no definite records of the channel catfish within 400 miles of Hudson's Bay. On the other hand there are many records to attest the abundance of the burbot in fresh waters adjacent to Hudson's Bay.

Both the channel catfish and the burbot grow to a length of three feet. A burbot three feet long should weigh about twelve pounds (as Pennant specified for his "mathemeg") but a channel catfish three feet long should weigh over 30 pounds, judging from length-weight data from South Bay, in northern Lake Huron (Fig. 1).

The channel catfish has eight barbels, of which there are four (not three) on the lower jaw; the middlemost are the shortest, not the longest. The burbot has three barbels, of which the middlemost is the longest. The incorrect phrase "on the lower jaw" may have been added by Pennant on the basis that beards are normally associated with lower jaws. There is nothing in his account of the "mathemeg" to suggest that he had personally seen a specimen. His color description, "the back is brownish: the belly grey," applies somewhat better to a burbot than to a channel catfish.

Walbaum (1792: 144) wrote:

33. GADUS, *lacustris*, Americanis *Mathemeg*, Anglis *Land. Cod.* Pennant arct. zool. introd. p. 191. Corpus tripedale, superne sub spadiceum, inferne griseum. Cirri tres in mandibula inferiore, quorum medius longitudine duos alios vincit.

It is obvious that Walbaum's Latin is merely a translation of Pennant's English account of the "mathemeg." Walbaum's contribution was to give it a proper Latin binomial name.

Rafinesque's (1818: 355) description of *Silurus punctatus* unequivocally applies to the channel catfish, which should now have restored to it the name *Ictalurus punctatus* (Rafinesque).

Richardson (1836) was apparently responsible for the interpretation of Pennant's

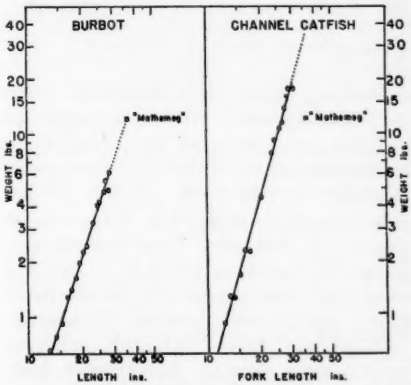


Fig. 1. Length-weight relationships of burbot and channel catfish. Samples from South Bay, Manitoulin Island, Lake Huron, Ontario. Note that the three-foot, 12-pound "mathemeg" of Pennant fits in with the burbot data, but not with the channel catfish data.

"mathemeg" as a channel catfish. He wrote (page 135):

60. 3. *Silurus* (*Pimelodus*) *borealis*. (Richardson.) The Mathemeg. Cod mathemeg. Penn., *Arctic Zool.*, Suppl., p. 115. No. 94. Intr., cxci. Silurus felis? Rich., Frank. Journ., p. 723. Le Chat. Canadian Voyageurs. Mathemeg. Crees.

The *mathemeg*, or *land cod* of the residents in the fur countries, is taken sparingly, during the summer months, in the lakes through which the Saskatchewan flows. It is the most northern American species of the family, but does not range higher than the 54th parallel. . . . Its Cree appellation signifies "ugly fish". A specimen which I brought home in 1821, is not now within my reach, . . .

Description of a specimen caught in Pine-Island Lake, lat. 54°N. . . . Anal large and long, terminating one third of its own length from the base of the *caudal*. The latter has a wide shallow fork with obtusely-rounded lobes. The length of the specimen, excluding the caudal, was thirty inches. Fins—D 1/6; P 1/6; V. 9; A. 25; C 17 3/3.

Much of Richardson's description is omitted above. His fish, however, was apparently a channel catfish—the most northerly record known to the writer.

Jordan and Gilbert (1883: 108) called the

channel catfish *Ictalurus lacustris* (Walbaum). These authors followed Richardson's lead in interpreting Walbaum's *Gadus lacustris* as a channel catfish. However, they must have had some misgivings as their synonymy reads:

(? *Gadus lacustris* Walbaum, Artedi Pisc. 1792, 144: ? *Pimelodus borealis* Richardson, Fauna Bor.-Amer. Fish. 135: ? *Amiurus borealis* Günther, v, 100: *Pimelodus nigricans* Le Sueur, Mém. Mus. v, 153, 1819: *Amiurus nigricans* Jordan, l.c. 83: *Amiurus borealis* Jordan, l.c. 84.)

However, Jordan and Evermann (1896: 137, footnote) said: "We see no reason for doubting the identity of the "Land Cod" or Mathemeg of the Hudson Bay region, with *Ameiurus nigricans*. This northern species, called *borealis* by Richardson, is the original *lacustris* of Walbaum." These authors considered the channel catfish to be two species, which they called *Ameiurus lacustris* (Walbaum) and *Ictalurus punctatus* (Rafinesque).

Hubbs and Allen (1943: 118) published their findings that the broad-headed individuals among channel catfish are the males, while the females are narrow-headed. Due to the great sex, age and geographic variations in this species, the Great Lakes males had been variously known as *Ameiurus*, or *Haustor*, or *Villarius lacustris* (and in the Mississippi Valley as *Ictalurus anguilla*), while the females have been generally called *Ictalurus punctatus*. Preliminary notice of these interpretations was given by Toner (1937: 3).

Since *Haustor* was proposed as a subgenus by Jordan and Evermann (1896: 135–37) with *Gadus lacustris* Walbaum as its type species, this name becomes a generic synonym of *Lota*.

Watkins (1938: 112) gave the Swampy Cree word for the ling (burbot) as "methi." It will be recalled that Forster and Pennant called it "marthy." These two names are apparently the listeners' phonetic attempts to write down the same Indian word, and the "mathe" of "mathemeg" appears to be the same word. The ending "meg" apparently means "fish," as in "tickomeg" or "atikameg" for whitefish. The Cree Dictionary has no word for the channel catfish, as one might expect for a species absent from the Hudson Bay region, and rare farther south in Cree territory.

## Subspecies

Hubbs (*in litt.*) has expressed the following opinion regarding the subspecies of *Ictalurus punctatus*. "It remains to be determined whether the geographical variation in *I. punctatus* is sharp enough to warrant the separation of a northern subspecies, from the Greak Lakes and Canada. If the separation can be made, it now seems evident that the southern subspecies would retain the name *I. punctatus punctatus* (Rafinesque) and the northern subspecies would be appropriately named *I. p. borealis* (Richardson)."

Hubbs and Schultz (1941: 18) indicated that the subspecies of *Lota lota* from the Hudson Bay region is the same as the Great Lakes form, now known as *Lota lota maculosa* (LeSueur, 1817). This should now become *Lota lota lacustris* (Walbaum, 1792). If the Great Lakes form should ever be shown to differ subspecifically from the Hudson Bay form, then the Great Lakes form would revert again to *L. l. maculosa*.

## Conclusion

Pennant's "mathemeg" and Walbaum's *Gadus lacustris* should be referred to the synonymy of the burbot, not to that of the channel catfish. The burbot of the Hudson Bay region, and the waters to the south and east, should be known as *Lota lota lacustris* (Walbaum) and the channel catfish should revert to its former name of *Ictalurus punctatus* (Rafinesque).

Five lines of evidence were followed to reach this conclusion: (1) Pennant was familiar with the differences between the cod and catfish families: he classified his "mathemeg" with the cods; (2) The channel catfish does not occur within 400 miles of the Hudson Bay region, whereas the burbot is abundant there; (3) Length-weight data for burbot and channel catfish indicate that the "mathemeg" was a burbot, not a channel catfish; (4) The number of "beards" (barbels) accredited to the "mathemeg" is correct for the burbot (which has three, one over each nostril and one in the center of the lower jaw), but not for the channel catfish (which has eight); (5) The Cree name "mathemeg" appears to have been derived from *methi* (burbot) and *meg* (fish).

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# Staining of Growth Rings in the Vertebrae of Tuna (*Thunnus thynnus*)

PAUL S. GALTSOFF

THE periodicity of growth in the bones of several commercial fishes of the North Sea was first demonstrated about 1903 by Heincke and Immerman who noticed that in plaice and in other species of fish a series of concentric rings is apparent not only in the otoliths but also in other bones of the skeleton. Heincke (1908: 97) pointed out that sharply defined areas of calcareous material, after a proper treatment, became apparent, without exception, in all the bones of the fishes he studied. According to this author, there is a complete correspondence in the sequence of growth lines, or circles, in various bones and scales of an individual fish. Illustrations of the growth rings in the operculum, cleithrum, ver-

tebra, and otolith of the plaice published by Heincke (*op. cit.*) seem to corroborate his conclusion.

Heincke and Immerman used the following technique: Bones were separated by cooking and soft tissues removed by gentle maceration. Following this, the bones were treated, first with "strong" (95°?) and then with absolute ethyl alcohol, and were defatted in benzine and ether. Drying in air completed the procedure. In certain cases, clarification in glycerine revealed the growth rings with greater clearness than could be attained in dry specimens.

Fig. 1. Caudal vertebra of tuna, alizarin stain, from a fish 104.5 cm. long, weighing 50 lbs. Actual dimension of the vertical diameter of the centrum is 2.2 cm. Drawn from a photograph.

Other authors who studied this problem in perch and codfish suggested the use of diluted writing ink (violet), rubber stamp ink, and picrocarmine in order to disclose the finest rings in small and thin scales and opercula of these fishes. It was claimed by Winge and Nilsson that picrocarmine produces differential staining of bones, the old deposits staining yellow, the new ones, pink.

In a study of material consisting of dried vertebrae of tuna fish, *Thunnus thynnus* (Linnaeus), collected during the summer of 1950 by the Fish and Wildlife Service in Cape Cod Bay, I failed to obtain satisfactory results with these methods. It was therefore necessary to develop a different staining technique which would make the growth rings clearly visible.[1]

The selection of the method used was based on the following considerations. It is known that some of the dyes of the anthraquinone group (alizarins) can be successfully used for gross staining of skeletons and for determining the presence of insoluble calcium salts in the cell contents. Lippman (1935) has shown that alizarin Red S is a specific stain for bone, and Hollister (1934) found that there is a great affinity of this dye to calcium phosphate, and that certain correlation exists between the intensity of staining and the concentration of this salt in the bone. It appeared, therefore, promising to try the alizarin method for revealing the growth rings in the vertebrae of tuna. The results (Fig. 1) fully justified this assumption. After several trials with various solutions I found that the following technique gave the best results:

*Material and Method.*—Dry vertebrae cut from fish bodies preserved in 10 percent formalin; soft tissues removed.

1. Rinse in distilled water.
2. Keep in 4 percent potassium hydroxide from 24 hours to 3–4 days depending on the size of the specimen. Prolonged treatment in KOH solution renders the preparation fragile.
3. Place in about 200 ml. of 0.1 percent alizarin stock solution in 2 percent potassium hydroxide for 24 hours or longer, at room temperature. Alizarin stock solution is prepared according to the following formula of Hollister:
   Alizarin Red S, saturated solution in 50 percent glacial acetic acid..... 5 ml.
   Glycerine, c.p., white..... 10 ml.
   Chloral hydrate, cryst., 1% aq. sol... 60 ml.
4. Rinse in water. Place in 4 percent potassium hydroxide for 12 to 48 hours.
5. Place in a mixture of 2 percent potassium hydroxide solution containing 40 percent of white glycerine for 1–2 days.
6. Increase the glycerine content to 80 percent. Keep 1–2 days.
7. Place in pure glycerine, change after 24 hours.
8. Place in fresh glycerine. Mount in glass jar.

Defattening of preparations in benzine or ether, preparatory to staining, was found to be unnecessary.

Since growth rings of the vertebrae are confined to the surface lining of the vertebra, the preparation should be very carefully

[1] The use of the term "growth rings" in this article does not imply that the circles revealed by staining are "annuli," for proof that the rings are laid down one per year is lacking.

handled during the dissecting and processing to avoid injury to the periosteum and underlying tissue.

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# The Philippine Species of the Cyprinid Fish Genus *Rasbora*

Martin R. Brittan and Bayard H. Brattstrom

THREE valid species of the southeastern Asiatic cyprinid genus *Rasbora* are found in the Philippine Archipelago, and these are restricted to the southern part. *Rasbora argyrotaenia* (Bleeker) is represented by a well-differentiated subspecies in the Culion-Busuanga-Palawan chain of islands; *R. taytayensis* Herre is known from the vicinity of Taytay, Palawan; and *R. philippina* Günther is known from Basilan Island and western and north-central Mindanao.

Two species of *Rasbora* have been described from Mindanao, *R. philippina* and *R. punctulata* Seale and Bean. In examining several series of specimens from Mindanao, we were unable to distinguish more than one species. These examples fitted both the original description of *philippina* (Günther, 1880: 54) and that of *punctulata* (Seale and Bean, 1907: 232, fig. 3). Several specimens of our series were submitted to Dr. Ethelwynn Trewavas, of the British Museum (Natural History), for comparison with the type of *philippina;* these same specimens were later sent to Dr. Leonard P. Schultz, of the U. S. National Museum, for comparison with the type of *punctulata*. Their examinations confirmed our suspicion that *punctulata* is a synonym of *philippina*.

The authors wish to thank Drs. Trewavas and Schultz for examining these type specimens, and Dr. Schultz for the loan of material from the U. S. National Museum (USNM). We also wish to thank Dr. George S. Myers, of the Stanford Natural History Museum, for making available for study the Philippine *Rasbora* in the collection of that institution. This represents but a small part of the extensive material amassed by Dr. A. W. Herre during his stay in the Philippines and his travels elsewhere. His collections have been instrumental in making the Stanford Museum outstanding among American museums in its representation of Pacific and Asiatic fishes.

The Philippine species of *Rasbora* may be distinguished by the following key (all measurements have been calculated):

A. Lateral line complete; 14 scale rows around middle of caudal peduncle; 9 scale rows over back in middle of caudal peduncle, between, but not including lateral line rows; 11–14 predorsal scales, usually 12 or 13.
  B. Body depth about 4.0 in standard length (3.6–4.5); snout pointed. Palawan, Culion, Busuanga..... .....*argyrotaenia everetti*
  BB. Body depth about 3.4 in standard length (3.1–3.8); snout blunt. Mindanao, Basilan..... .....*philippina*

AA. Lateral line incomplete, not extending beyond anal fin, and often not reaching it; 11 predorsal scales; depth 3.3–3.5. Palawan.....*taytayensis*

*Rasbora argyrotaenia everetti* Boulenger

*Rasbora everetti* Boulenger, 1895: 187 (original description; Palawan; type in British Museum).
*Rasbora argyrotaenia* Herre, 1924a: 1568 (Busuanga; Lake Manguao and Puerta Princesa, Palawan); 1924b: 267 (description), 705 (reference); 1934: 20 (Culion; Concepcion, Busuanga); Roxas and Martin, 1937: 43 (reference).
*Rasbora punctulata* Fowler, 1941: 813 (in part; Palawan, Busuanga).

The following specimens of this subspecies were examined. (Unless otherwise noted, all material is from the Stanford Natural History Museum):

Busuanga Island: Wayan Creek, 70; San Nicolas, 60; Concepcion, 12; Singai, 70; Port Calton, Pangauron River, USNM, 14; Port Uson, Malbato River, USNM, 46; Exact locality not given, 5.

Culion Island: Karig Malan River, 100+; Creek flowing into Halsey Harbor, 150+.

Palawan Island: Malatagao and Camino Rivers at Puerta Princesa, USNM, 68; Iwahig River and tributaries near Puerta Princesa, USNM, 59; Nakoda Bay (tributary stream, not specified), USNM, 2.

DESCRIPTION.—A large slender *Rasbora* with a pointed snout. Depth 4.0 (3.6–4.5), width 7.4 (6.8–8.3), head 3.8 (3.4–4.5) in standard length. Eye 3.5 (3.0–4.0), snout 3.2 (2.8–3.6), interorbital 2.5 (2.2–2.7) in head length. Pharyngeal teeth 2,4,5—5,4,2. Length of caudal peduncle 2.1 (1.6–2.4) times its depth. Lateral line complete, perforating 31–32 scales (31–34), including one or two on base of caudal fin.

Predorsal scales 13 (12–14). Scales in transverse line from dorsum to belly, in front of dorsal and anal fins, 9, including mid-dorsal and mid-ventral scale rows. Five rows above the lateral line row, 3 below it. Scale rows around middle of caudal peduncle 14, 9 of which lie over the back between the lateral lines. Dorsal ii, 7, originating over the 12th (11th–12) scale of lateral line, its height 1.1 (1.0–1.2) in body depth. Dorsal-hypural distance when carried forward, falling at nostril, or a little forward of it. Anal iii, 5, originating over 18th (17th–18th) scale of lateral line, its height 1.3 (1.2–1.4) in body depth. Pelvics ii, 8, originating at 10th (10th–11th) scale of lateral line, 1.4 (1.3–1.5) in head, 5.4 (5.2–5.9) in standard length. Pectorals i, 14 (i, 13–i, 15), not quite reaching pelvics, 1.2 (1.0–1.4) in head, 4.9 (4.2–5.7) in standard length. Caudal lobes pointed, the longest rays 2.1 (2.1–2.2) times shortest, 0.1 longer than head. The largest specimen measured 133 mm. standard length (about 160 mm. total length), but usual adult size is from 70–110 mm.

COLORATION.—In formalin, brownish above, yellowish brown below. Reticulate pattern distinct. A prominent, dark longitudinal stripe from the opercle to the base of the caudal fin, at a level with upper part of the eye, and about as wide as the pupil posteriorly, narrower anteriorly. This stripe is bordered dorsally for its entire length by the axial septum, which is pigmented from the caudal base almost to the opercle A thin, poorly-developed dorso-lateral stripe runs along the lower margin of the 2nd. longitudinal scale row. Between these two stripes is a longitudinal light area which is poorly defined. (In *Rasbora*, this area typically forms a metallic gold or copper streak in life.) There is a fairly prominent mid-dorsal streak occupying the middle third of the vertebral scale row from the occiput to the caudal base. The supra-anal pigment is in the form of a weak streak along the anal base, but is often absent. There is a series of dark, vertical, almost chevron-shaped streaks down the lateral-line scale row and along the next scale row above. These markings are located under the posterior part of each scale and consist of pigmentation of the posterior part of the fold forming the scale pocket, but the markings are unconnected; they are apparently isolated elements of the reticulate patterns, and extend posteriorly at least to above the anal, and often to the caudal, though quite weak posteriorly. Fins faintly dusky, the caudal with a narrow, diffuse blackish hind-border.

DISTRIBUTION AND RELATIONSHIPS.—The Philippine subspecies of *R. argyrotaenia* is found on Culion, Busuanga, and Palawan Islands. As presently recognized, *arygrotaenia* appears to be a composite species. The separation of the several nominal species now masked under this name is being attempted by the senior author. The working-out of the subspecies of *argyrotaenia* awaits the study of further collections.

Fowler (1941: 814) has referred a large series of specimens collected by the ALBATROSS to *R. punctulata*, a synonym of *R. philippina*. All of the specimens listed, except those from Basilan Island and Zamboanga, are referable to *R. a. everetti*. The Basilan and Zamboanga specimens (9234, 9236, and 9240) are *philippina*.

Through the courtesy of Dr. Trewavas we have been able to compare specimens of the Philippine *argyrotaenia* with a photograph of the type of *R. everetti* Boulenger (type locality: Palawan), thus establishing their co-identity.

*R. a. everetti* apparently reached its present

range from Borneo when Palawan, Culion, and Busuanga were connected with it and with each other as part of emergent Pleistocene Sundaland. Dickerson (1941: 21), citing Herre's study of the fishfauna of Palawan (in Dickerson, et al., 1928: 242–247), considers Palawan to have been connected with Borneo during the early, but not the late, Pleistocene, because more than the one Bornean species, *R. argyrotaenia*, would be present in Palawan. Though six other cyprinid species of three other genera are present in Palawan, all are specifically distinct from their closest relatives in Borneo. For a discussion of various phases of the Tertiary and Quaternary geological history of Sundaland see de Terra (1943), Molengraaf (1930), and Umbgrove (1930, 1938, and 1949); for zoogeographical aspects of the problem see de Terra (1943), Dickerson (1941), Dickerson, et al. (1928), Hooijer (1951), and Mayr (1945).

### *Rasbora philippina* Günther

*Rasbora philippina* Günther, 1880: 54 (original description; type in British Museum; Pasananca, near Samboangan (Zamboanga), Mindanao). Herre, 1924a: 1568 (Zamboanga and Cayagan de Misamis, Mindanao); 1924b: 268 (Titunod R., Mindanao; Cayagan de Misamis, Mindanao); 1934: 20 (Kolambugem, Lanao Province, Mindanao). Arnold and Ahl, 1936: 214, text fig. (life colors; Philippines). Roxas and Martin, 1937: 43 (reference).

*Rasbora punctulata* Seale and Bean, 1907: 232, text fig. 3 (original description; Zamboanga; type (holotype) USNM No. 57842, 3 inches). Roxas and Martin, 1937: 43 (reference).

*Rasbora punctulata* (in part) Herre, 1924a: 1568 (Zamboanga); 1924b: 266 (Zamboanga; Basilan Island), 705 (reference). Fowler, 1941: 813 (Isabela R., Basilan; Zamboanga R., Zanboanga).

The following material of this species was studied:

Mindanao: Six miles northeast of Zamboanga 87; Marata Bogan, 30 km. east of Kolambugan (Kolambugem), Lanao Province, altitude about 1,000 feet, 9; Zamboanga River, Zamboanga, USNM, 25.

Basilan: Isabela River, USNM, 20.

DESCRIPTION.—A medium-heavy, middle-sized *Rasbora* with a rounded snout. Depth 3.4 (3.1–3.8), width 7.4 (6.4–8.4), head 3.8 (3.4–4.1) in standard length. Eye 3.1 (2.8–3.6), snout 3.6 (3.2–4.1), interorbital 2.7 (2.2–3.1) in head. Interorbital space arched. Pharyngeal teeth 2,4,5–5,4,2. Lateral line complete, perforating 30–31 (29–32) scales. Predorsal scales 11–13. Scales in transverse line from dorsum to belly 9, 5 above lateral line row, 3 below; to anal origin 6 + 1 sheath scale. Scale rows around middle of caudal peduncle 14, 9 of which lie over the back between the lateral lines. Predorsal distance 1.9, preanal distance 1.5, prepelvic distance 2.2 in standard length.

Dorsal ii, 7, originating over 11th or 12th scale of lateral line, its height 1.2 (1.0–1.4) in body depth. Dorsal-hypural distance, when carried forward, falling at or slightly behind nostril. Anal iii, 5, originating at 16th or 17th scale of lateral line, its height 1.5 in body depth. Pelvics ii, 8, originating at 9th or 10th scale of lateral line, 1.4 (1.3–1.5) in head, 5.4 (5.0–5.7) in standard length. Pectorals i, 12 or i, 13 (rarely to i, 15), not quite reaching pelvics, 1.2 in head, 4.4 (4.2–4.6) in standard length. Caudal lobes pointed, the longest rays 2.1 (1.9–2.3) times the shortest, 0.1 longer than head.

The largest specimen examined measured 64 mm. standard length, 82 mm. total length. Seale and Bean (1907: 233) gave the size of their largest specimen of *R. punctulata* (here synonymized with *R. philippina*), the holotype, as "3 inches" (about 74 mm.); through the courtesy of Dr. E. A. Lachner and Robert Kanazawa, of the U. S. National Museum, it has been determined that this specimen is 58.5 mm. in standard length, and about 74 mm. total length. This species is much smaller than *R. a. everetti*, for the usual size range is about 50–60 mm. standard length.

COLORATION.—Dark brownish on the dorsum, medium brown on the upper sides, the flanks and belly light yellowish brown; this is the typical coloration, but some populations (Stanford No. 38109, 3 specimens from Zamboanga) are pale in color, the over-all effect being pale yellowish brown, with the dorsum only very slightly darker. This may be due to preservation. A dark lateral band runs from opercle to caudal base, being broadest anteriorly (here also slightly arched dorsally), and most intense posteriorly. This band is prominent in larger specimens, though not so intense as in Philippine specimens of *R. argyrotaenia*, or in *R. lateristriata*, *R. taeniata*, etc., and is less distinct in young specimens. In light-colored populations it is also rather diffuse.

A mid-dorsal stripe from occiput to caudal

root, being most distinct, narrower, and more sharply defined anterior to the dorsal. Posterior to that fin it broadens and becomes less sharply defined, whereas anteriorly its width is one-half to three-fourths of the vertebral scale row. Reticulate pattern very pronounced in the darker populations, most so in larger specimens, the elements beneath the 3rd, 4th, and 5th longitudinal scale rows, especially, forming a series of transverse streaks or blotches. Small specimens and members of paler populations show the same effect, though faintly. The supra-anal pigment presents an elongate blotch or thin streak along the base of the anal fin, at the bases of the rays. The sub-peduncular streak is absent or very diffuse. Fins hyalin, except for a slight grayish or yellowish gray wash on their proximal portions, strongest on the caudal.

DISTRIBUTION AND RELATIONSHIPS.—This species is known only from the western and north-central portions of the island of Mindanao in the Philippines and from nearby Basilan Island. It is a member of the *argyrotaenia* species group, and is most closely related to the Philippine subspecies (*R. a. everetti*). *R. philippina* seems almost certain to be a derivative of *argyrotaenia*. The distribution of the forms is clear cut; *philippina* is found only on the islands of Mindanao and Basilan, whereas *R. a. everetti* is confined to the islands of the Palawan-Culion-Busuanga chain. The ancestors of *philippina* apparently reached Mindanao from Borneo at a time when the two islands were connected or only very narrowly separated during the Pleistocene or late Tertiary (J. W. Durham and R. W. Kleinpel, *in litt.*).

### *Rasbora taytayensis* Herre

*Rasbora taytayensis* Herre, 1924b: 264 (original description; creek near Taytay, Palawan).

DESCRIPTION (after Herre).—Dorsal ii, 7; anal iii, 5; pectoral i, 12; pelvics i, 7. Scales in longitudinal series 26–28; 5 scale rows above lateral line row (scale rows below lateral line not given); predorsal scales 11. Dorsal profile nearly straight, ventral profile strongly convex. Depth 3.25–3.57; head equal to depth or shorter, 3.5–3.77 in length; eye large, 3.0–3.5 in head, and from ⅓ to ⅓ longer than the short, blunt snout; interorbital space flat, 2.2–2.55 in head, from ¼–⅓ wider than eye. Lips thin, subequal, or the lower projecting. Symphyseal knob prominent. Origin of dorsal at 10th scale of lateral line, nearer caudal than snout, nearer pelvic than anal, its height slightly less than head-length. Pectoral not reaching pelvics, 1.1–1.3 in head. Origin of pelvics opposite 9th scale of lateral line, not reaching anus. Anal height 1.2–1.37 in head, its least depth 1.25–1.57. Caudal deeply forked, longer than head, longest rays less than twice as long as shortest. Nine rows of scales between the lateral lines, counted over the back in front of dorsal. Lateral line never extending beyond anal, often not reaching it. Reaches maximum (total?) length of 50 mm.

COLORATION (after Herre).—In alcohol, silvery brown, very dark above, paler below. A narrow black stripe from nape to caudal. A blackish or dark silver line along the side on the posterior half of body, with a black circular spot at base of caudal. Below this is a broad, dark band, best developed anteriorly and composed of many fine dots. A dark brown bar behind the posterior margin of gill opening. Scales margined with many fine dark spots. A band of many black spots along the base of anal. Fins colorless, or their rays more or less dark dotted.

DISTRIBUTION AND RELATIONSHIPS.—This species is known from six spawning females, 38–50 mm. long, the basis of the original description, collected in a pool in the bed of a dry stream along the trail between Taytay and Malampay Sound, and 164 specimens, 18–45 mm., collected in a creek near Taytay, Palawan. All of these were apparently lost when the Japanese destroyed the building which housed the Philippine Bureau of Fisheries during the battle for Manila, in February, 1945.

Dr. Herre considered this species to be most closely related to *R. semilineata* Weber and de Beaufort (1916: 80). Structurally, this would seem to be true; the position of both *semilineata* and *taytayensis* within the genus *Rasbora* is in doubt, however. Both show, especially in the reduction of the lateral line and in their small size, affinity to *pauciperforata*, *taeniata*, and *borapetensis* and their relatives. In the less strong reduction of the lateral line, the reduction of the predorsal scales from the usual 12 or 13 for the genus, and the decrease in longitudinal scales from the generic average of 29–30, they resemble the *trifasciata-bankanensis-rutteni* complex.

It is impossible to tell if *semilineata* and *taytayensis* have a close common ancestor, or are examples of recent convergent evolution from more distantly related precursors. We hope that topotypes of *taytayensis* may be recollected soon, and specimens once more made available to ichthyologists.

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# Spawning Habits and Early Development of the Mountain Whitefish, *Prosopium williamsoni,* in Montana[1]

C. J. D. Brown

THE mountain whitefish is one of the most abundant game fishes in Montana. Very large populations are present in the Yellowstone River and upper Missouri River, of the Missouri River drainage, and in the Flathead River and Clark Fork River, of the Columbia River drainage. Almost none of the cold valley streams is without them but they are not as a rule found in the small mountain tributaries. While *Prosopium williamsoni* (Girard) has been regarded as little better than a sucker by the average fisherman, there is at present a growing respect for this fish. It is sought after most vigorously in winter when the majority of waters are closed

[1] Contribution from Montana State College Agricultural Experiment Station Project No. MS844-42, Paper No. 256, Journal Series.

to trout fishing and when whitefish are more easily caught.

A study of the food habits of this species in Montana has recently been published (Laakso, 1951) and investigations on its growth rate, distribution and taxonomy are in progress. Observations on the spawning habits and early development were begun in 1947 and have continued to the present. These investigations have been confined largely to the Gallatin, Yellowstone, and Madison Rivers.

TABLE I

ACTUAL EGG COUNTS OF 21 WHITEFISH COLLECTED IN THE YELLOWSTONE, GALLATIN AND MISSOURI RIVERS

| Total length, inches | Weight, ounces | Number of eggs |
|---|---|---|
| 10.2 | 6 | 1,426 |
| 10.3 | 7 | 2,160 |
| 10.4 | 6 | 1,532 |
| 10.4 | 8 | 1,940 |
| 10.7 | 7 | 1,955 |
| 11.0 | 7 | 1,470 |
| 11.1 | 10 | 4,321 |
| 11.2 | 8 | 1,773 |
| 11.2 | 8 | 2,114 |
| 11.7 | 10 | 4,106 |
| 11.7 | 9 | 3,465 |
| 12.2 | 10 | 3,261 |
| 12.9 | 12 | 3,242 |
| 13.1 | 12 | 4,131 |
| 14.0 | 13 | 3,700 |
| 15.0 | 16 | 5,360 |
| 15.2 | 16 | 4,494 |
| 15.5 | 20 | 5,191 |
| 16.0 | 20 | 5,377 |
| 17.0 | 24 | 7,271 |
| 19.5 | 48 | 24,143 |

The writer is indebted to several students who helped in making collections and to Professor Harold Watling for assistance in interpretation of embryological stages.

NUMBER AND SIZE OF EGGS.—The number of eggs produced by whitefish is generally correlated with the length and weight of the fish (Table I). With some exceptions, the larger the fish, the more eggs it will produce. However, one female with a total length of 11.1 inches produced approximately 2.5 times more eggs than another which was 11.2 inches long. Egg counts of 21 individuals taken just before spawning (egg sacs still intact) show a variation from 1,426 to 24,143 (Table I). The smaller number was produced by a fish weighing six ounces which was 10.2 inches in total length and the largest by a three pound specimen, 19.5 inches long. The average for the 21 specimens was 4,401, or 5,343 per pound of fish. Simon (1946) reported that whitefish from Jackson Lake, Wyoming, produced an average of 6,885 eggs per pound of fish. That the ovaries make up a substantial part of the body weight is described by Sigler (1951). He gave 18.8% as the average. The ovaries of one large female from the Yellowstone River made up 21.8% of the body weight.

Simon (1946) reported that mountain whitefish eggs total 912 per fluid ounce. Diameter measurements based on a sample of 50 water-hardened eggs showed an average of 3.7 mm. with a range of 3.1 to 4.2 mm. Sigler (1951) gave 1.94 to 2.12 mm. as the diameter of whitefish eggs and reported that egg size increased with the size of the fish.

Most of the whitefish become sexually mature in their third year of life although a few mature in their second year.

SPAWNING.—Observations were made during the spawning seasons of several years for the purpose of witnessing the behavior of the fish at that time. No marked mass movement or migrations were observed and no unusual concentrations of fish were seen in areas known to be used for spawning. The whitefish in lakes do move up tributary streams to spawn (Simon, 1946). Large runs come into the traps on the South Fork of the Madison River from Hebgen Lake, along with brown trout spawners. Concentrations of whitefish are reported in the shallower water near shore in Cliff Lake during the spawning season but no evidence has been presented to show that they spawn there. A small number of whitefish move into some of the tributary streams from the larger rivers. On the Yellowstone River, such tributaries as Mission Creek, Tom Miner Creek and Mol Heron Creek are used. Other comparable tributaries in the same general area are not used and the reason for this is not evident. Spawning whitefish were found only in the lower 300 to 500 yards of these streams.

Whitefish spawn in the gravel and rubble riffle areas of the streams. There seems to be little or no selection of bottom materials. An

abundance of eggs, in various stages of development, has been found in bottoms ranging from fine gravel to coarse rubble. Water depths varied from five inches to four feet. Spawners undoubtedly use depths much greater than four feet but such areas could not be sampled with our equipment. Eggs were usually most numerous in areas adjacent to strong currents; some were found in the bottom directly below rapid surface velocities, and some where water movement was hardly perceptible.

No evidence was found that whitefish prepare nests as do trout. There was little or no noticeable disturbance of the bottom in the areas used. The only means of detecting spawning beds was by searching for the eggs.

Regular sampling of areas in the West Gallatin River at a place near Manhattan, Gallatin County, showed that spawning did not occur in 1949 until after October 14 when water temperatures had decreased to 42° F. Eggs were abundant in the gravel here on October 28. Several whitefish captured on this date had partially spawned, but none completely, and others were still "green". By November 10, spawning was about over and most of the females caught at this time were completely spawned out. Several still retained a few eggs. All whitefish collected in this area on November 17 (water temperature 40° F.) were without eggs. Several of them showed marked recovery from spawning as evidenced by their ovaries and general body condition.

The peak of whitefish spawning in streams at higher elevations occurs at a later date. Large numbers of "ripe" fish were captured in the South Fork of the Madison River on November 14, 1950, when the water was 36° F.

A collection of 25 whitefish taken on October 16, 1949, in the Yellowstone River 17 miles below Livingston, Park County, showed 12 ripe females, 12 green females and seven ripe males. On October 20, 1951, a collection of 40 adult whitefish from the same area included 32 females, 12 of which were green, 18 in various stages of spawning and two spawned out. The eight males of this collection were ripe and appeared to be partially spent. On November 3, 1950 (water 41° F), all females captured in this area were spawned out and the males were nearly so.

Attempts were made to observe the spawning act of whitefish during three successive spawning seasons in areas known to be used. All observations made during daylight hours were unsuccessful. Whitefish were seen congregating in shallow water on several occasions, usually just before dark and this led the writer to suspect that spawning occurred at night.

With the assistance of spotlights, night observations were made on Mol Heron Creek. Whitefish were seen to spawn in this creek just after dark on November 2, 1951 (water 32° F.), at a place about 50 yards upstream from its confluence with the Yellowstone River. Spawning fish were not much disturbed by a light when partially shaded from it. They moved

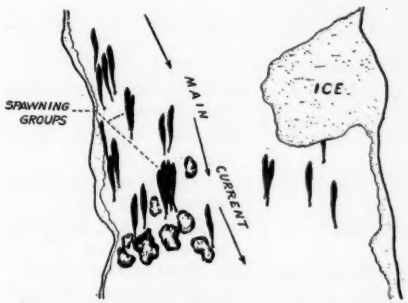


Fig. 1. Sketch showing cross-section through Mol Heron Creek with spawning whitefish.

away from a strong beam of light held directly on them, however, and could be herded to either side, upstream or downstream, depending upon how the light approached them.

About 30 whitefish were in the immediate area under observation (approximately 100 square feet). They were in groups of 2 to 5 with several fish remaining apart at least for a time. We had no means of determining the sex composition of the groups although males were known to be predominant as evidenced by a sample of fish taken in the area after observations were completed. All males and females were ripe, for eggs and milt came from these fish even with careful handling. The greatest concentration of fish occurred in water about one foot deep just to the side of the main current (Figure 1).

Fish were just holding their position against the current and at intervals the individuals within a small area would move close together so that their bodies were in contact, and as they did so they came almost to rest on the

bottom. They remained in this position from 2 to 4 seconds and then would move apart, sometimes separating and moving up or down stream. There were no rapid or violent body movements. Individuals from one group were observed to join others and the process was repeated. It was not possible to see eggs or milt extruded but freshly laid eggs (not yet water-hardened) were collected on a screen held directly behind one of these groups. In one instance about 25 eggs were collected. A few water-hardened eggs and small pebbles were also collected on the screen at the same time, indicating that some of the eggs in the bottom were dislodged in the process.

TABLE II

DEVELOPMENT OF WHITEFISH EMBRYOS IN WEST GALLATIN RIVER NEAR MANHATTAN, MONTANA, DURING THE WINTER OF 1949–50

| Date | Water temperature, in °F. | Early stages of development |
|---|---|---|
| 10/28/49 | 47 | Newly fertilized eggs to well formed blastoderm |
| 11/10/49 | 41 | Blastoderm to early neural axis |
| 11/17/49 | 40 | Late neural axis to lateral enlargement of head |
| 12/ 4/49 | 33 | Late neural axis to early eye; some pigmentation |
| 12/16/49 | 32 | Late neural axis with anterior dorsal thickening of body. Eye medium development, lens partly to wholly formed |
| 1/20/50 | 32 | Eye lens large. Posterior body fully formed. Pigmented lateral line |
| 2/15/50 | 36 | Dorsal of head and sides of body pigmented. Entire body raised from yolk |
| 3/ 4/50 | 42 | Yolk much reduced. Body fully formed and pigmented. Hatching just begun |

PREHATCHING DEVELOPMENT.—Samples of whitefish eggs were taken at fairly regular intervals throughout one winter from a gravel riffle area of the West Gallatin River near Manhattan in order to ascertain the rate of development under natural conditions. At the beginning, embryos were not all in the same stage of development (Table II) because spawning occurred over about a two week period. However, by January 20, all embryos were fairly uniform in their development. The first eyed embryos were found in the December 4 collection and the first hatching individuals were secured on March 4.

HATCHING AND LATER STAGES.—Spawn was artificially taken from 25 whitefish collected on the South Fork of the Madison River on November 14, 1950. After fertilization, eggs were allowed to stand in river water for about an hour before being transported to the Bozeman Fish Hatchery. In the evening of this same day, eggs were placed on drip trays in the hatchery. The water flowing through the trays had a temperature of 52° F. and varied from this no more than a ±2° F. during the period of development. Dead eggs were picked off on December 6, at which time all living embryos were eyed. The majority of these fish hatched on December 20 and had absorbed all their yolk by December 29. Hatching thus occurred 36 days after fertilization at a water temperature of about 52° F.

TABLE III

SIZE OF WHITEFISH FRY AND FINGERLINGS

| Place | Date | Total length (mm.)* | |
|---|---|---|---|
| | | Range | Average† |
| Gallatin river | 3/ 4/50 | 11.3–12.2 | 11.7 |
| Gallatin river | 4/14/50 | 14.7–17.0 | 15.8 |
| Gallatin river | 5/21/50 | 26.0–29.6 | 27.7 |
| Gallatin river | 6/ 9/50 | 23.8–40.6 | 35.3 |
| Gallatin river | 10/ 2/49 | 86.0–111.1 | 94.5 |
| Yellowstone river | 3/23/50 | 13.5–15.2 | 14.4 |
| Yellowstone river | 7/21/48 | 37.6–64.4 | 52.3 |
| Yellowstone river | 10/22/50 | 112.3–126.5 | 120.3 |
| Hebgen reservoir | 6/12/49 | 42.4–58.0 | 51.4 |
| Hebgen reservoir | 7/ 7/49 | 53.4–85.1 | 66.1 |

* All measurements on preserved specimens (10% formalin).
† Ten specimens in each sample.

Practically all of the whitefish hatched in the West Gallatin River near Manhattan between March 4 and 28 (water 40 to 42° F.). A tremendous hatch of whitefish was observed in the Yellowstone River, 17 miles down stream from Livingston, on March 23, 1951 (water 42° F.). Many of the eggs kicked from the gravel on

this date hatched on the screen which trapped them.

After considerable searching, many whitefish fry with yolk sacs still visible were found in the Gallatin and Yellowstone Rivers during late March. They were present along the shore where the water was very shallow (2 to 6 inches), in small, well protected pockets created by rubble or boulders and in all back waters connected to the main stream.

A collection of fry taken from the West Gallatin River on April 14, 1950 (water 48° F.), had an average total length of 15.8 mm. (Table III). Another sample from this same area on May 21 had an average length of 27.7 mm. By June 15, all of the fingerling whitefish which had occupied the quiet areas near shore had disappeared and no amount of effort could locate them in water which could be waded or seined. Collections of fingerlings (average total length 94.5 mm.) were made in the deep pools of the West Gallatin River on November 2, 1949, with the assistance of electrical shocking equipment. Whitefish fingerlings deserted the shallow shore waters of the Yellowstone River in late July when they were about 55 mm. in total length. Fingerlings which averaged 120.3 mm. in total length were captured in deep pools on this stream on October 22, 1950. A study of their scales showed them to be young of the year.

If our samples are representative, whitefish fry and fingerlings grow most rapidly in Hebgen Lake of the Madison River and least in the Gallatin River.

### Literature Cited

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# Herpetological Notes

NOTES MADE BY DR. EDWARD HALLOWELL.—The library of the Academy of Natural Sciences of Philadelphia possesses a set of Holbrook's *North American Herpetology*, second edition, containing numerous pencil notes made by the eminent herpetologist Dr. Edward Hallowell. The author feels that these notes are of sufficient historic interest to warrant transcription before they become completely obscure with age.

Volume I, under the heading of *Cistuda carolina* Edwards; notes at bottom of page 33 to be appended to word 8, line 18: "Major LeConte states that none of the Box Tortises in Florida have more than three toes upon the posterior extremities."

Volume III, under the heading of *Crotalus durissus* Linnaeus; notes at bottom of page 12 to be appended to end of line 2: "Col. McCall states that one of the soldiers on lying down was bitten four times in the back by a durissus, but recovered—the bite was in the month of March. They are said to be most dangerous in August.—E. H."

Volume III, under the heading of *Crotalus adamanteus* Beauvais; notes at bottom of page 18 to be appended to end of last line: "Col. McCall states that he has known several mules to be bitten by the adamanteus, and recover.—E. H."

Volume III, under the heading of *Crotalophorus milarius* Linnaeus; notes at bottom of page 28 to be appended to end of last line: "Col. McCall informed me that one of the privates attached to his regiment was killed by the bite of a milarius.—E. H."

Volume III, under the heading of *Crotalophorus tergeminus* Say; notes at bottom of page 30 to be appended to end of line 24: "found by Col. McCall in the Orapi Indian Country, and in New Mexico, near the Rocky Mountains in sandy, partly prairie—where there was but little grass."

Volume III, under the heading of *Brachyorrhos amaenus* Say; notes at bottom of page 117 to be appended to word 6, line 2: "neighborhood of Philadelphia."

Volume V, under the heading of *Salamandra longicauda* Green; notes at bottom of page 62 to be

appended to end of line 23: "Found also in the banks of the Wissahickon (new road 2 miles from Chestnut Hill—with S. erythronota)—E. H."—ROBERT SUTCLIFFE, *Academy of Natural Sciences of Philadelphia, Philadelphia 3, Pennsylvania.*

TERRESTRIAL HIBERNATION OF THE BULLFROG, *RANA CATESBEIANA* SHAW.—There are many references attesting to the aquatic propensities of the bullfrog, *Rana catesbeiana*. Wright (1914, Carnegie Instit. Pub., 197: 86) said it is "truly an aquatic form"; Dickerson (1913, The Frog Book: 228) said it is "more thoroughly aquatic than any of the other frogs of northeastern North America"; Walker (1946, Ohio State Mus. Bull., 1 (3); 69) said it is the "most aquatic of our frogs"; Breckenridge (1944, Reptiles and Amphibians of Minnesota: 76) said it is "highly aquatic and seldom ventures out of water for any distance." Furthermore, this frog is said to hibernate in water (Morgan, 1939, Field Book of Animals in Winter: 360; Pope, 1947, Amphibians and Reptiles of the Chicago Area: 118).

On March 5, 1951, I found a bullfrog hibernating underneath the litter in an oak-hickory woods on the Edwin S. George Reserve, Pinckney, Michigan. The situation was unusual in two respects: (1) a "strictly" aquatic frog was hibernating on land; and (2) this frog, in all probability, moved overland to its hibernating site from a permanent marsh approximately 350 feet away. The frog occupied a soil pocket 5 inches long, 4½ wide and 2½ deep, situated in a natural surface depression about 3 feet in diameter. There was a 3½-inch litter mantle, but no soil, covering the animal. Crouched in its hibernating position, it measured 4 inches from snout to vent.

I next visited the site on March 20 and placed a Taylor Six's self-registering thermometer underneath the litter next to the frog on a level with its back. A snowfall of about 1½ inches had occurred the previous day. The temperature beneath the snow was 31°F; at a soil depth of 2½ inches, 33°; underneath the litter, next to the frog, 32°; four and one-half feet above the ground, 27°.

A week later, on March 27, when I temporarily removed the litter, the animal stirred and moved its eyelids. There were ice crystals in the adjacent soil surrounding the frog. The maximum and minimum temperatures in the frog's niche for the week interval, March 20–27, were registered as 42° and 23°. During the same week the air temperatures went as low as 13° and as high as 54°.

When I again visited the site, on April 3, I found that the frog had left its niche. During the interval of March 27 to April 3, the maximum temperature in the soil pocket was 39° and the minimum, 37°. The highest air temperature for the week was 60° and the lowest, 30°. At the time these registered readings were observed on April 3, the air temperature was 39°.

Wright (*op. cit.*: 78) says that the earliest record for the appearance of the bullfrog near Ithaca, New York, is May 11 (1901). The maximum temperature of the previous day was 68° and the maximum on May 11 was 74°; he had no spring records of this species until a maximum of at least 68° was attained both on the day previous to and the day of the first appearance. The bullfrog that I observed left its hibernating quarters during a period when the air temperature (4½ feet above the ground) never got above 60° and the niche temperature never exceeded 39°. That the hibernating animal was not the victim of some predator is certain since the wire cage placed over the site had not been disturbed. The frog managed to extricate itself from the cage by crawling underneath the free ends which had not been forced into the soil.

These observations show that (1) the frog had moved overland a considerable distance from its still existing aquatic habitat to reach the hibernating site; (2) hibernation took place on land; (3) the temperature of the frog's niche dropped far below freezing (23°) at least once even though the period was late winter; (4) hibernation was terminated at an early date and during an interval when the maximum temperature in the soil pocket never exceeded 39°; and (5) the site was abandoned during a period when air temperatures were 60° or less.—KURT BOHNSACK, *Department of Biology, Swarthmore College, Swarthmore, Pennsylvania.*

NOTES ON AMPHIBIANS FROM OKLAHOMA AND NORTH DAKOTA.—I reported (1950, COPEIA (2): 152) that *Microhyla carolinensis* and *M. olivacea* from localities 15 miles apart in northeastern Oklahoma were completely distinct with no evidence of intergradation. It is now possible to state that in the vicinity of Locust Grove, Mayes County, Oklahoma, the ranges of the two species overlap at least 3 miles with no evidence of intergradation. Typical *carolinensis* was taken June 15, 1951, in a roadside ditch 1½ miles west of Locust Grove. On the same day *carolinensis* was taken 1½ miles east of Locust Grove in a roadside pool where *olivacea* was taken June 26, 1948. While *carolinensis* was calling in many places in the Oklahoma Ozarks on June 10 and 15, *olivacea* was not heard along the western border of the Ozarks; presumably the showers of this period were not heavy enough to stimulate breeding activity of the more xeric species.

The broad expanse of Grand River, which runs along the western border of the Ozarks in northeastern Oklahoma, would seem to be a formidable

barrier to the dispersal of microhylid frogs. With the taking of *carolinensis* one mile west of Salina, Oklahoma, June 23, 1951, it becomes evident that the eastern species is west of the river and the western species is east of the river.

An adult *Ambystoma annulatum* was found under a small post-oak log at the edge of a hillside seep 9 miles northeast of Sallisaw in Sequoyah County, Oklahoma, April 19, 1951. In the same general vicinity were found *Plethodon glutinosus*, *Eurycea griseogaster* and *Triturus viridescens louisianensis* (red eft stage).

Clearing and staining of specimens of *Typhlotriton* from Bat Cave (5 miles south of Kansas, Adair Co., Okla.) confirm that the population is *nereus*, and not *spelaeus* as previously indicated (Blair, 1939, Copeia (2): 108–109). However, a large larval population in a brook 3 miles northeast of Locust Grove appears to be entirely *spelaeus*. No adults of *spelaeus* have been found in this vicinity.

*Hyla versicolor* was not listed by Wheeler (1947, American Mid. Nat., 38 (1): 162–90) as a North Dakota frog. A chorus of this species was found 10 miles south of Fargo on the night of June 20, 1938. A specimen taken at that time is No. 52440 in the collection of the American Museum of Natural History.—Albert P. Blair, *Department of Zoology, University of Tulsa, Tulsa 4, Oklahoma.*

BEHAVIOR OF CAPTIVE LOGGERHEAD TURTLES, *CARETTA C. CARETTA* (LINNAEUS).—Three loggerhead turtles, *Caretta c. caretta*, loaned by the South Boston Aquarium to the U. S. Fish and Wildlife Service Aquarium, Woods Hole, Massachusetts, were observed from June 20 to September 3, 1951. The turtles, averaging about 15 inches in carapace length, were kept in a glass fronted tank approximately 6 feet long by 4 feet wide and 4 feet deep. A fresh supply of aerated sea water circulated continuously.

Unlike captive specimens reported on by Hildebrand and Hatsel (1927, Proc. Nat. Acad. Sci. Washington, 13: 374–377) these individuals were quite docile and attempted to bite each other only during the excitement of feeding or when one attempted to usurp the resting site of another. If a hand stirred the surface they would often approach and make a slow, deliberate snap at it, undoubtedly mistaking it for food since they were often fed in this manner.

Their diet consisted of a variety of dead fish, dead squid, spoiled lobster meat, soft parts of mussels, whelks, and various other mollusks. Once, bodies of deer mice (*Peromyscus*) were offered but not eaten. Horseshoe crabs (*Limulus*), about 9 inches long excluding the telson, were placed in the tanks but were soon incapacitated when the turtles bit off their legs. Although the turtles would frequently seize and shake a *Limulus* by its carapace, they seemed unable to crush through the tough exoskeleton.

A loggerhead with a carapace length of 24 inches was captured in a fish trap near Woods Hole. Its stomach contained portions of intact vertebrae of two fish about 4 or 5 inches long, several large pieces of the sulfur sponge (*Cliona celata*), remains of a spider crab (*Libinia*) with a carapace width of about 3 inches, some flesh, and several pieces of vegetation.

The daily activity of the captive turtles appeared to be about equally divided between swimming and resting on the bottom of the tank. When resting, they always selected a corner and would lie completely motionless with the head thrust into the corner, eyes open or half shut, and flippers extended in about the normal midstroke position of swimming. They were alert in this position and the slightest movement from above the water by the observer would usually bring them from their resting site to the surface. No amount of motion or rapping on the glass from the outside appeared to disturb them. Possibly they slept in this same position, since on one occasion they were observed at night by dim light and were found in their corners with eyes tightly closed. They were slower to rouse than during the daylight hours.

A certain amount of territoriality was apparently concerned in the resting behavior. Usually a given turtle occupied the same corner of the tank while at rest. Once, the regular occupant of a corner delivered a vicious snap at the head of another that attempted to occupy the same site.

The rate of respiration of the three animals was variable. When swimming actively in the tank they surfaced for air on an average of once every 2.1 minutes; the observed extremes ranged from 15 seconds to 24 minutes. When resting, the average time between breaths was 12.7 minutes, although they did remain on the bottom as long as 25 minutes. —James N. Layne, *Department of Conservation, Cornell University, Ithaca, New York.*

EARLY TRANSFORMATION OF THE GREENFROG, *RANA CLAMITANS* LATREILLE.—All reports in the literature indicate that in nature the greenfrog (*Rana clamitans*) spends at least one winter in the larval stage which lasts 370 to 400 days. A few even suggest that occasionally two winters are passed as tadpoles.

Because of some fortunate events, evidence contrary to the above was found about 2½ miles east-northeast of Ann Arbor, Michigan. In 1948, the summer and fall were dry—so dry that all the water

in the ponds on the study area was evaporated, killing myriads of tadpoles. The only ranids that were observed to complete their larval development that year were a small number of leopardfrogs (*R. pipiens*) and pickerelfrogs (*R. palustris*). The bottoms of the ponds were so thoroughly desiccated that deep clefts formed in the sun-baked soil, producing conditions which made it impossible for any tadpoles to survive there. By measuring the area and the average depth of the masses of dead and dying tadpoles in the last rapidly disappearing puddles and by counting the number of individuals in a representative sample, it was estimated that 60,000 to 75,000 were present.

The next winter and spring the ponds were refilled. Then, in the summer and fall of 1949, a large number of fully developed tadpoles and transforming and recently transformed greenfrogs were taken in them. An estimate, determined from quadrat samples, indicated that on August 24 there were 10,700 newly metamorphosed frogs present. Details of this population will be given in a later paper.

It is highly improbable that so many tadpoles could have found their way into the ponds which were connected in tandem by narrow canals. The last pond overflowed into a small stream about 180 yards from the nearest site where transforming greenfrogs were observed. The overflow into the stream was the only avenue by which tadpoles could migrate into the ponds but its characteristics were such as to prevent this movement. About twelve feet from the stream the water in the outlet passed downward into a muskrat burrow through which it entered the stream. A vertical descent of ten inches occurred at the place of entrance into the muskrat burrow, providing an insurmountable barrier to tadpoles which might have been in the stream. At no time was the water observed to be high enough to permit tadpoles to get above this critical descent, although it is possible that such a level was attained early in the spring or immediately after late spring downpours. However, at such times the water was very swift and usually subsided in a few days. As the tadpoles are weak swimmers, and since only 11 were collected in the stream in 1948 and five in 1949, it is unlikely that many, if any, got into the ponds from that source.

From the above data it seems conclusive that the larvae of the greenfrog do transform in the same season that the eggs are laid. I do not think that this early transformation is peculiar to this area alone; in fact, there is every reason to conclude that it is usual for eggs laid early in the spring. Eggs laid late in the breeding season, however, produced tadpoles which did not metamorphose until the following year. It is only because large numbers of such tadpoles were observed in the winter that previous authors thought overwintering to be the typical event for all larvae. Also it is only because of the fortunate (for me) drying of the ponds that there was opportunity to observe this feature of the life cycle. Similarly, in some newly constructed ponds in Iowa, Klimstra (1949, Copeia (3): 231) observed that the bullfrog (*R. catesbeiana*) required but one winter, instead of two as was formerly thought, for the completion of its larval development.

The results of Ting (1951, Copeia (1): 82) serve to confirm my observations of the early transformation of greenfrogs. He artificially fertilized greenfrog eggs in the laboratory and 92 days later some of the resulting tadpoles transformed.—Bernard Martof, *Department of Biology, University of Georgia, Athens, Georgia.*

A RANGE EXTENSION FOR THE WATERSNAKE, *NATRIX SIPEDON PLEURALIS* COPE.—The range of the midwest watersnake is recorded as extending from South Carolina westward around the southern extremity of the Appalachian Mountains, Mississippi, Arkansas, and southern Missouri, and northward to southern Illinois and southern Indiana (Stejneger and Barbour, 1943, Check List North American Amphib. Rept., Ed. 5: 162). Recent collections made by Tulane University field crews have revealed the presence of *Natrix s. pleuralis* in Tangipahoa and Washington parishes, eastern Louisiana, far to the south of any previously recorded localities. Thirty-three specimens from the Tangipahoa and Pearl River systems, examined by the author, are referable to this subspecies. Although Dellinger and Black (1938, Occ. Pap. Univ. Ark. Mus., 1: 27–31) report *Natrix s. pleuralis* from the southwestern

Table I

Variation in the Characteristics of *Natrix s. pleuralis*

(Averages in parentheses; extent of lateral bars and interspaces determined by counting scales along third scale row).

| Locality | Dorsal body blotches | Complete transverse bands | Mid-body dorsal scales | Ventral scales | Lateral bar extent | Interspace extent |
|---|---|---|---|---|---|---|
| Varnado.. | 22–31 (26.3) | 6–13 (9) | 23 | 131–140 (135.7) | 1.5–3.0 | 2–6 |
| Angie.... | 21–29 (25.3) | 1–10 (6.2) | 23 | 133–138 (135.2) | 1.5–3.0 | 2.5–6 |
| Enon..... | 23–26 (24.5) | 5–10 (7.5) | 24 | 135–137 (136) | 1.5–2.5 | 3–5 |
| Amite.... | 21–30 (25.3) | 1–10 (6.2) | 23 | 134–139 (136.7) | 1.5–3.5 | 2–5 |

corner of Arkansas, recent collecting in Louisiana adjacent to this area has failed to indicate the presence of this subspecies.

For the sake of convenience and in order not to obscure possible population differences, the extent of character variation in each of the four localities represented is treated separately (Table I). The specimens are in the collections of Tulane University and bear the following catalogue numbers: Washington Parish, Pearl River at Varnado—2590, 2600, 3282, 5399, 6240, 6283, 13777; Washington Parish, Pearl River at Angie—12201, 12203–04, 12206, 12209–11, 12220, 12239–40, 12247, 12347, 12352, 12422; Washington Parish, Bogue Chitto River at Enon—13904 (2); Tangipahoa Parish, Tangipahoa River near Amite—13793 (9).

An interesting problem, arising with the discovery of the populations of *Natrix s. pleuralis*, is the occurrence of *Natrix s. confluens* and *Natrix s. fasciata* in the same drainage. No evidence of intergradation between *Natrix s. pleuralis* and the other two subspecies is apparent at this time. Future investigation may reveal distinct habitat differences which permit the overlapping of the range of the three subspecies. The presence of *Natrix s. pleuralis* in the Gulf coastal region is apparently another example of an essentially northern reptile that has followed southward drainages toward the Gulf.

The author is indebted to Roger Conant for suggestions during the preparation of this paper.—ROBERT E. GORDON, *Department of Zoology, Tulane University, New Orleans, Louisiana.*

AN OBSERVATION OF SKIN-SHEDDING IN *PLETHODON C. CINEREUS*.—While feeding some redback salamanders one evening, I noticed one of the larger specimens in a large crystallizing dish push its snout up against the glass of the side. With a sudden downward shove, the skin was rolled back to the neck region before I really understood what was happening. This partiuclar specimen had just swallowed a fly maggot, and I supposed it might have been wiping its mouth on the glass when the operation started.

As I watched further, the salamander's body seemed to expand just in front of the rolled-up skin, and the skin started gliding back along the body which remained stationary. When the base of the forelimbs was reached, the salamander laid its forelimbs back close against its body, and, pushing forward with its hind legs while the skin was caught on a small piece of rotted wood, it slipped the skin off over the legs. It seemed to "work" at removing the skin for a short period, pause, then begin again. The skin was pushed back along the body to the base of the hind legs by a combination of expanding the body in front of the old skin and pushing the body along among the chips of wood. The hind legs were laid back flat against the base of the tail, and local, lateral wriggling motions of the body in front of the tail seemed to force the skin over the thigh and shank. Then, unlike the method used in freeing the forelegs, each hind leg was forcibly pulled forward out of the remaining old skin which had covered the foot. The skin was rolled off from the tail by simply dragging it as the salamander moved about over the debris in the dish. At no time did the animal make an attempt to aid in the removal of the old skin by using its jaws.

Another maggot was eaten by this same salamander immediately after the moult had been completed. It would therefore seem that the process of moulting in this species is not nearly so drastic an event as that which occurs in the shedding of the skin by snakes. The entire process was accomplished in about 15 minutes, with no apparent preliminary or terminal resting period. No attempt was made by this specimen to eat its own cast skin, as Noble (1931, Biology of the Amphibia: 140) indicates many species may do.—L. M. BARTLETT, *Department of Zoology, University of Massachusetts, Amherst, Massachusetts.*

*HYLA SEPTENTRIONALIS* DUMERIL AND BIBRON ON THE FLORIDA MAINLAND.—The range of *Hyla septentrionalis* in the United States has been cited as the Florida Keys by various authors (Carr, 1940, Univ. Florida Pub. Biol., Sci. Ser., 3 (1): 62; Wright and Wright, 1949, Handbook of Frogs and Toads: 338; and Myers, 1950, COPEIA (3): 212). Trapido (1947, Herpetologica, 3 (6): 190) records a northeastward extension of range along the arc of the Keys, having taken this frog on Upper Matecumbe Key.

Collecting herpetological material for the University of Michigan Museum of Zoology in the spring and summer of 1951, the writer took breeding adults of *Hyla septentrionalis* in Miami, Dade County, Florida. These specimens constitute, as far as known, the first definite records of the giant treefrog from the mainland of Florida, although Wright and Wright (*loc. cit.*) state that the range extends as far as Matecumbe, Florida, "and farther northward." Presumably this implies the Keys alone, and not the mainland.

A single specimen (♂, UMMZ 103178, snout-vent length 50 mm.) was taken in Miami in the evening of June 18, 1951, at the intersection of Red Road and NW 7th St., by Charles Huber. The area is a low-lying field which is flooded after heavy rains, and supports a low growth of grass, which is removed in strips for sodding. On the afternoon of June 18, a heavy rain with high winds occurred, and in the field were calling great numbers of *Hyla*

*squirella, Bufo quercicus, Bufo terrestris* and *Microhyla carolinensis*.

After a late afternoon downpour on July 9, 1951, a rock pit which is used for trash disposal was visited at NW 27th Ave. and NW 42nd St. by J. Porter, R. Prior and the writer. Large numbers of *H. squirella* were calling from the bottom of the rock pit, and the chorus was deafening. At this locality seven *H. septentrionalis* (UMMZ 103179) were taken: one female (73 mm.) and six males (49–52 mm.). None of these individuals was heard calling, probably because of the din caused by the *H. squirella*. An adjacent portion of the rock pit bottom supports a small permanent pond and growth of cattails, and from this area *Hyla cinerea* was heard calling in small numbers. *Hyla septentrionalis* was found only in water about 1 inch deep in thick grass and among the debris and trash on the floor of the pit.

The giant treefrogs were kept alive overnight, and at 9:00 AM on July 10, the frogs were placed in a gallon jar with an inch of water. At this time the female and a male were in amplexus. By 10:00 AM the female had laid a large clutch of eggs and the pair had separated. At 4:00 PM the eggs were in typical yolk plug stage. On the morning of July 11 at 9:15, a few of the eggs had reached neural groove stage, and by 1:30 PM five tadpoles had hatched. The balance of the eggs did not go beyond the yolk plug stage. Thus, from laying to hatching, a period of not more than 27½ hours was required. These five tadpoles were kept in a culture dish until September 3, 1951, at which time the two remaining individuals were preserved; no evidence of metamorphosis was at hand at that date.—ALBERT SCHWARTZ, *Museum of Zoology, University of Michigan, Ann Arbor, Michigan.*

ADDITIONAL NOTES ON THE RANGE OF *RANA GRYLIO* STEJNEGER IN SOUTH CAROLINA.—*Rana grylio* was first recorded from South Carolina by Wilfred T. Neill (1947, COPEIA (3): 206). His specimens were from near the Beaufort-Colleton county line, about 7 miles east of Yemassee, Jasper County. Recent collecting has extended the known range of this frog some 85 miles northeastward along the coast to southern Georgetown County. There are now specimens in the collection of the Charleston Museum from the following localities: Jasper Co., near Switzerland, No. 48.107.3 (3 specimens); Beaufort Co., U. S. Highway No. 17 at the Combahee River, No. 49.55.1 (3); Dorchester Co., Biven's Backwater, 17 miles WNW of Charleston, No. 51.45.9 (4); Charleston Co., Mayrant's Reserve, 19 miles NE of Charleston, No. 51.45.7 (4); Georgetown Co., Kinloch Plantation, 15 miles S of Georgetown, No. 51.45.8 (4). This frog has also been heard calling at Ashepoo, Colleton County; Goose Creek and Cypress Gardens, Berkeley County; and Blake's Reserve, 8 miles NE of McClellanville, Charleston County.

The frogs from Dorchester, Charleston, and Georgetown counties were collected between June 7 and June 13, 1951. Most of them were located by their occasional calls during the day, and all were collected at night. On June 16, a trip was made to Horry County to look for this species. It was not heard calling during the day or at night, and no habitat was seen similar to that in which this frog had been found elsewhere. Although the range of this frog may extend farther north than Georgetown County, it seems to be limited by the presence of old rice reserves and similar habitats, where it is found commonly in lower coastal South Carolina.

I wish to express my thanks to Julian Harrison and John Quinby for help in collecting specimens. —THOMAS M. UZZELL, JR., *Museum of Zoology, University of Michigan, Ann Arbor, Michigan.*

POPULATIONS OF *XANTUSIA VIGILIS* THREATENED WITH EXTERMINATION.—The need for constant alertness in conservation is emphasized once more by a new threat to some of our wild life, this time to the populations of one of our most interesting reptiles, *Xantusia vigilis*, the viviparous yucca nightlizard.

Probably no single American lizard has been studied from so many different approaches as has this species. There have been studies on the endocrinological aspects (Malcolm Miller), color changes (Atsatt and Caswell), embryological (Heimlichs), parasitological (Amrein, in a paper now under preparation), parturition (Cowles), and high temperatures and fertility (Cowles). Many other ecological and distributional studies have been reported. Other investigations along these and similar phases of research are no doubt being carried out at the present time at various institutions, and it is also known that these small lizards are sometimes collected or purchased in order to provide food for larger species of carnivorous reptiles. All together, the demands for living specimens of this little lizard have led to offers, largely to high school students, of as much as fifteen cents apiece, and apparently this price is an effective inducement for extensive collecting activity.

It is quite possible that the actual destruction of the individual lizards, especially by high school collectors, might not be the most serious factor in this activity, but all too often these amateurs (and sometimes college students and even faculty members engaged in legitimate investigation) fail to replace the logs, boards, rocks, and so forth,

which are required as shelters, and this negligence may in the long run be more deleterious than the collecting itself. As the result of all of the interest focused on *Xantusia*, it has become an increasingly frequent and alarming experience to travel a hundred miles or so to our nearby desert in order to procure needed specimens, only to find that, over scores of acres, all available *Xantusia* shelters have been overturned and rarely replaced, as would be necessary to preserve the habitats. Numerous areas totaling many hundreds of acres of land which was once richly supplied with these lizards have been virtually depopulated in recent years.

There can be little doubt that the worst offenders in collecting and in the destruction of habitats and niches are those who are engaged in this activity for commercial reasons. I have recently learned that some boys had taken close to one hundred specimens of *Xantusia* a day, equal to fifteen dollars at the currently reported rate, and wherever they have been active it is doubtful if five percent of the lizard shelters could sustain even a single residual animal. This is wholesale destruction and is completely inexcusable.

It is not known how long a time is required to convert a freshly turned or a newly fallen Joshua tree log to the stage of semi-burial and decay needed by these lizards, but an estimate of five to ten years is probably not excessive; it is not unreasonable, therefore, to expect the virtual extermination of this animal over very large areas where it is, or recently has been, exceedingly abundant.

The value of these animals in research of various kinds, as illustrated by the foregoing sketchy list of what has already been accomplished, and the probability that even more new studies will be envisioned in the future, would seem to point to the need for immediate cessation of all commercial collecting. In part, this can be expedited by refusal of our biologists throughout the country to purchase any of these animals.

With the removal of the profits motive, the remaining individuals of *Xantusia* should have some chance of starting the slow process of repopulation (these animals bear only one or, at most, two young per year); but even without the present commercial collecting, it is the duty of every teacher, high school or college, to preach conservation of these animals and the perpetuation of their habitats and ecological niches, and to demonstrate the methods of search and replacement that will conserve our animals to the greatest degree.

Even if it were possible to procure the enactment of laws affording protection to these and other reptiles, experience shows that without understanding and sympathetic response to such laws, little or nothing can be gained by having them enacted. Education and immediate cessation of commercial exploitation seem to proffer the greatest opportunity for the success of steps necessary for the preservation of this interesting little reptile.—RAYMOND B. COWLES, *Department of Zoology, University of California, Los Angeles, California.*

BIPEDAL LOCOMOTION IN THE IGUANA, *IGUANA TUBERCULATA*.—Although the bipedal type of locomotion is known to occur among many of the smaller, long-limbed, fast moving lizards, this gait has not been observed very frequently in the larger, living forms. Stirling (1912, Trans. Roy. Soc. South Australia: 36) records bipedal locomotion in the giant Australian varanid (*Varanus giganteus*), by stating "that when travelling at their topmost speed the forelimbs are raised from the ground, so that their gait then becomes bipedal."

In the afternoon of September 1, 1940, while walking along the side of the golf course of the United Fruit Company's station at Puerto Armuelles, Panamá, we came upon a four-foot *Iguana tuberculata* out on the green fairway. Since it was our first iguana, we attempted to approach it in order to observe it more closely. The lizard, with its long heavy body only a few inches above the ground, made off rapidly over the greensward on all four legs. To our surprise, after running for a short distance in this fashion, it rapidly raised its forelegs against its chest, and, holding them there, continued its speedy progress on hind legs alone. No marked attempt was made to elevate the fore part of the body farther while running in this fashion. The two-legged movement of this iguanid is similar to that described by Stirling for the large varanid. It is remarkable that such large, short-legged and heavy-body lizards as these two are not limited to quadrupedal means of progression. —ARTHUR SVIHLA and RUTH DOWELL SVIHLA, *Department of Zoology, University of Washington, Seattle 5, Washington.*

# Reviews and Comments

DIE BINNENGEWÄSSER BD. XVIII VERBREITUNGSGESCHICHTE DER SÜSSWASSERTIERWELT EUROPAS. By August Thienemann. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 1950, 809 pp., 249 figs., $22.80.—It is timely to call attention to this comprehensive tome by August Thienemann, Dean of European limnologists, in the light of the success of recent books on ecology which testify the genuine interest of American biologists in zoogeography.

Ichthyologists will find useful the detailed accounts comprising nearly 100 pages concerned with postglacial facts about coregonid fishes, the restricted occurrence of *Cottus* [= *Myoxocephalus*] *quadricornis*, the island-like constriction of *Hucho hucho* and *Umbra lacustris*, and other distributional phenomena. The profuse references and discussions on the influence of glaciation on distribution will be informative to students of North American taxonomy. Such glacial-edge types as *Gasterosteus aculeatus*, *Coregonus*, and *Salmo* (*Salvelinus*) *alpinus* receive moderate attention. For those who would introduce more foreign species into North America there is fair warning in Thienemann's analysis of the 1905 introduction and rapid spread of the muskrat which has become a pest over all of central Europe. *Eupomotis* [= *Lepomis*] *gibbosus* has multiplied in the Hungarian Danube area, and is successful in some parts of Italy. Rainbow trout are dominant in many places over the native brown trout. Smallmouth bass have not spread to the detriment of local fishes although they reproduce naturally in several lowland alpine lakes. The largemouth bass and the black bullhead occur only spottily.

Modern principles of ecology and limnology relevant to zoogeographical studies comprise an eighth of the book. In dedication, Prof. Thienemann honors the memory of eight of his former students and colleagues who fell in two world wars, of whom Fritz Geyer, Alfred Buschkiel, Erich Wasmund and Friedrich Krüger are well known to American aquatic biologists.—Arthur D. Hasler, *University of Wisconsin, Madison 6, Wisconsin.*

DIE NAHRUNG DER MEERESTIERE BD. I, OF HANDBUCH DER SEEFISCHEREI NORDEUROPAS. Heft 5a, Teil I–II (I. Einleitung—II. Das Plankton), by Hagmeier, A. and C. Künne, 103 illustrations; Heft 5b, Teil III–IV (III. Die wirbellosen Boden und Nektontiere. IV. Beziehungen der Ernährung zur Verbreitung der Arten und der Gemeinschaften der Bodentiere), by Arthur Hagmeier and Clemens Künne, 156 illustrations. Stuttgart, Schweizerbart'sche Verlagsbuchhandlung, 1950–51.—Recent visitors to northern Europe report a post-war renaissance of fishery science. Revival of the "Handbuch" series of the calibre of this one verifies these observations.

To identify fish food organisms a marine fishery biologist must have at hand a volume each on algae, diatoms, Protozoa, Crustacea, larval invertebrates and fishes, in addition to a general textbook on invertebrate zoology. Wrapped in one small parcel and profusely illustrated (many new drawings and photographs of whole animals and anatomical views) are the dominant pelagic and demersal adult and larval forms that are important food for aquatic animals of the northern seas. Moreover, discussed in concise but oldfashioned German scholarliness, are modern concepts of ecological relationships of plankton and bottom organisms in addition to their distribution.

A section on larval fishes and their food concludes Sections I and II. Sections III and IV describe the bottom organisms (Protozoa, Metazoa (from sponges through the arthropods) and includes the tunicates. Food chains, feeding patterns, distribution, niches, associations, and importance of the organisms as fish foods make up part III.

All in all, this work on the food of marine animals would make a useful textbook for a course in marine food chains and their ecology. Normally a large series of references would be needed for a study table. Here is a complete and concise assemblage of facts from traditional and modern references found scattered in numerous journals and reports and in many languages. Moreover, it is an indispensable tool for a field man not having access to a fairly complete library.

Other parts of Vol. I (Naturbedingungen des Lebens in Meere) in translation are: 1. The areas and depths of the sea by K. Kalle; 2. The natural properties of waters by K. Kalle; 3. Bottom deposits of north European seas by O. Pratje; 4. The rooted plants of north European seas by W. Nienburg. 5a and 5b are reviewed above; and 6. The economy of the sea by K. Brandt and J. Reibisch.—Arthur D. Hasler, *University of Wisconsin, Madison 6, Wisconsin.*

TROPICAL FISH AS A HOBBY. By Herbert R. Axelrod. McGraw-Hill Book Co., New York, 1952: xiv + 264 pp., many photos, 2 color-plates.

$4.00.—The enormous public interest in keeping tropical fishes in home aquariums engenders occasional books upon the hobby. This is one of the better ones, for it answers the basic questions of the beginner who wants to keep his fish healthy and perhaps breed a few of them. However, whether it will (as its author hopes) also be of use to the advanced aquarist and as a reference text for teachers and students of biology, is, in the reviewer's opinion, somewhat doubtful. Although there are a couple of excellent and important articles by Myron Gordon and James Atz reproduced as chapters, the general organization and balance of the book leave something to be desired, the illustrations are not always well chosen, and the author doesn't know some of his fishes too well. As a beginner's guide, the book could have been shortened to advantage. To be useful also to advanced aquarists it needs revision by a skillful aquarist-writer more able than its author. The price, when compared with that of W. T. Innes's finely illustrated treatment of the same subject, is too high.—GEORGE S. MYERS, *Stanford University, California.*

DER FISCH IN DER LANDSCHAFT. BEITRÄGE ZUR ÖKOLOGIE DER SÜSSWASSERFISCHE. By Werner Ladiges. Second edition. Braunschweig, Gustav Wenzel und Sohnore, 1951: 182 pp., 104 text-figs.—Just before the second world war, Dr. Ladiges published a long and interesting series of articles on fish ecology in the Wochenschrift für Aquarien- und Terrarienkunde. The reviewer heard that these articles were reprinted in book form after the war had begun, but reserve stock of the book must have been destroyed for he has never been able to obtain a copy. Now a new, enlarged and rewritten edition is available, published in December, 1951.

Although semi-popular in style, this small book is one of the most important publications in the whole field of fish ecology, for it represents what is essentially a pioneer contribution to the hitherto almost unknown ecology of the smaller freshwater and brackish water fishes of tropical America, Africa, Asia and Australia. Moreover, the book is written from an unusual point of view—that of a trained ecologist who works for a commercial aquarium fish firm and whose success as a collector, shipper, caretaker and breeder of live fishes depends to a large extent on his exact personal knowledge of fish habitats and ecology in far scattered parts of the world.

The book is divided into two sections. The general section deals with *lebensraum*, food, and propagation. The special section begins with the general features of the inland waters of central Europe and their fishes. Following this are chapters dealing with specific ecological observations on the fresh waters and fishes of tropical Asia, Africa, South America, Central and North America, of caves in various places, and, finally, of Australia. Most of these chapters consist to a considerable degree of personal observations by the author, illustrated with photographs and diagrams of habitats, with water analyses, and with tables giving the habitat preferences of long lists of species. In nearly all instances the information is either new or has not previously been gathered together in usable form.

There are numerous things about the book open to criticism. Except for landscape description, both above and below the surface, chemical analyses of single water samples, temperatures, pH figures, and habitat preferences, there is little basic ecology of any one species. However, it is evident from the title of the book that the author intended no more, and it should be emphasized that the ecology of most of the fishes mentioned has hitherto been an utter blank. Perhaps more to be criticized is the author's passing over some fine and carefully done ecological work in the very areas of which he treats, for example that of Carter and Beadle in the Gran Chaco and British Guiana, and of several writers in India. His general bibliography at the end is very restricted. However, he has done a great service in combing out the exceedingly numerous references to fish ecology in the German aquarium fish literature, a rich source of information on fish breeding habits and ecology that is almost unknown to most ichthyologists. It is most unfortunate that the book has no alphabetical index. Despite these criticisms, this book should be in any general ichthyological library.—GEORGE S. MYERS, *Natural History Museum, Stanford University, California.*

NOTE ON AVAILABILITY AND PRICE OF *FISHES OF THE WESTERN NORTH ATLANTIC*, MEMOIR I, PART I.—In a recent catalogue of books on botany and zoology, issued by Eric Lundberg of Walpole, N. H., this book was listed at a price of $15.00. To those who may be interested in purchasing the book, either now or in the future, we wish to point out that the established price is $10.00 and that it may be purchased at this price plus postage from the Sears Foundation for Marine Research, Bingham Oceanographic Laboratory, P. O. Box 385, Yale Station, New Haven, Conn. An adequate supply was printed so that the book would not go out of print for some years to come.—YNGVE H. OLSEN, *Yale University, New Haven, Connecticut.*

HANDBOOK OF SOUTH AMERICAN INDIANS. Julian H. Steward, Editor. Vol. 6, Physical

anthropology and cultural geography. (Bureau of American Ethnology, Bulletin 143, vol. 6.) Government Printing Office, Washington, D. C., 1950. $5.00.—While a review of an anthropological work may seem out-of-place in COPEIA, most naturalists who have collected in South America have some curiosity regarding the indigenous human fauna. Moreover, this great handbook, of which only the seventh volume (indexes) remains unpublished, would interest any but a dull naturalist, and the present volume contains two sections of direct value to zoologists.

Carl Sauer's "Geography of South America" (pp. 319-344) is an excellent brief summary for the naturalist, with fine climatic and vegetational maps. Raymond Gilmore's "Fauna and Ethnogeography of South America" (pp. 345-464) forms a useful introduction to the fauna and the best existing general compendium on aboriginal use of Neotropical animals. Among the vertebrates, it is best when treating of the wild and domesticated mammals (the author is a mammalogist) but somewhat weak and uneven for "herps" and especially fishes, upon which many of the Indians depend even more than on mammals. There is a considerable account of remora-fishing, which is interesting but relatively unimportant, but only bare mention of the wide and important use of piranha teeth for cutting instruments (for hair, wood, darts, etc.), and almost none at all of the widespread fear of (and use of protective devices, for both male and female, against) the candirú entering the urethra. Nor are several important foodfishes (pacú and most marine ones) even listed, and the literature sources, especially Brazilian, have not been sufficiently explored. Yet even the fish section is interesting.—GEORGE S. MYERS, *Natural History Museum, Stanford, California.*

ANIMAL EVOLUTION, A STUDY OF RECENT VIEWS OF ITS CAUSES. By G. S. Carter. Xv + 368 pp., 62 figs. Sidgwick and Jackson, Ltd., London, 1951. 30 shillings ($4.50 in the U. S.).—We now have many excellent modern books on certain phases of animal evolution, by Goldschmidt, Dobzhansky, Huxley, Rensch, Mayr and Simpson, but the only one of them which attempts to cover the subject in a comprehensive way (Huxley's "Evolution, the Modern Synthesis") is scarcely a text to put into the hands either of the college biology student or of the older zoological specialist who wishes to refresh his evolutionary knowledge in a general way. This new member of the Sidgwick and Jackson "Text-books of Animal Biology" fills the want, and takes an honored place among its fellows—the same author's "General Zoology of the Invertebrates," de Beer's "Vertebrate Zoology," Elton's "Animal Ecology," and others.

The author, known to ichthyologists through his physiological work on South American fishes, has done an excellent job in reducing to brief and readable form the essentials of the large, growing, and often abstruse recent literature on evolution. The subject matter ranges from paleontology and major evolutionary trends to life-histories and the mathematics of selection. Incidentally, Carter's species definition pleases the reviewer far more than does Mayr's, for it admits the difficulties more fully. All in all, this book can be recommended as the best general text-book on animal evolution in any language now in print.—GEORGE S. MYERS, *Natural History Museum, Stanford University, California.*

MARINE GEOLOGY. By Ph. K. Kuenen. John Wiley and Sons, Inc., New York, 1950: x + 568 pp., 246 text-figs., 2 pls. $7.50.—Those scientific workers who have to do with the sea, whether they be geologists, oceanographers, fishery biologists, or biogeographers, must know this book. More comprehensive than Shepard's recent "Submarine Geology," the present work is also less of a text than a general survey of a rapidly developing new field, part and parcel of geology yet perhaps quite as much a segment of oceanography. Its author, professor in the University of Groningen, Holland, is especially familiar with the marine geology of the Malay Archipelago, which holds so many biogeographical problems inextricably linked with geological history, and this experience is evident in his selection of examples. Yet other parts of the world are not neglected.

The chapters concern (1) physical oceanography, (2) the sea basins, (3) the Indonesian deep-sea depressions, (4) sources and transportation of sediments, (5) the formation of marine sediments, (6) coral reefs, (7) geomorphology of the sea floor, and (8) eustatic changes of sea level. The book is excellently edited, illustrated, and printed, with selected chapter-bibliographies and an index. The only thing the reviewer misses are some zoogeographical references to a few papers which would have greatly reinforced some of the author's statements.—GEORGE S. MYERS. *Natural History Museum, Stanford University, California.*

FAUNA OF THAILAND. By Chote Suvatti. Department of Fisheries, Bangkok, Thailand; 1100 pp., frontispiece. 1950.—This book reminds me of a bitter cold day in the winter of 1933-34 when Chote Suvatti, finished with his undergraduate work at Cornell and in Washington for a brief period to study Siamese fishes under my direction, spent the evening with me talking over his future in Siam. Many years have rolled by and the then-young student is now in charge of the fisheries department of his homeland. Moreover, he has now

produced a work which, while not perfect, will be of the greatest help to anyone beginning any type of biological work on the fauna of Thailand.

This is a bibliographical checklist of the Thai fauna, from Protozoa to Mammalia (but omitting terrestrial arthropods), arranged systematically, with a chronological bibliography and an alphabetical index. While it is certain that some hundreds of references in the very scattered zoological literature on Siamese animals have been overlooked (especially in general group-monographs such as Simpson's "Monograph of the Naiades" and Parker's "Microhylidae"), the lists are surprisingly complete for vertebrates. Especially useful is the careful coverage of references in the "Journal of Natural History Society of Siam." Mr. Suvatti must receive the congratulations of all naturalists interested in the Indo-Malayan fauna, and not least those of the reviewer.—GEORGE S. MYERS, *Natural History Museum, Stanford University, California.*

PRIMER CONGRESO NACIONAL DE PESQUERIAS MARITIMAS E INDUSTRIAS DERIVIDAS. Mar del Plata, 24-29 Octubre 1949. Vol. 1, Recomendaciones, 102 pp. Vol. 2, Trabajos Presentados, xiv + 323 pp. Imprenta y Casa Editora "Coni," 684 Calle Peru, Buenos Aires, Argentina. 1950.—These are the proceedings of the first "National Congress of Marine Fisheries and Related Industries" to be held in Argentina. They deserve notice if for no other reason than to bring them to the attention of those interested, for proceedings of this type are seldom easily obtainable for very long after publication. Although the congress was apparently devoted in large part to the fishery industry, these proceedings illustrate most forcibly the plain fact that modern methods in fishery biology and fishery management are very poorly understood throughout Latin America, even though modern ideas of a general nature are beginning to penetrate. One author, Z. Popovici, demonstrates a real grasp of the problems to be faced. However, all the papers are of use to anyone interested in Latin American fisheries, and the proceedings should be in any marine fisheries library.—GEORGE S. MYERS, *Natural History Museum, Stanford University, California.*

FAUNA ET FLORA ADRIATICA. VOL. I. PISCES. By Tonko Soljan. Institut za Oceanografiju i Ribarstvo fnr Jugoslavije (Split, Jugoslavia); quarto; 437 pp., numerous text-figs. and diagrams. 1948.—Although this book is written in what is apparently the Serbo-Croat language and, despite its size and format, is purely an elementary identification-manual and not a treatise in systematic ichthyology, it seems worth while to notice it if only because Mediterranean and especially Balkan fish publications often remain unknown to American workers. The bulk of the book is devoted to a totally artificial but somewhat ingenious key to the fishes of the Adriatic Sea, with one or more line drawings of each species and a superabundance of stylized diagrams showing exactly how to place the dividers or fingers or both upon a specimen of each and every species in order to get the proportions and counts that will identify it. The result is an identification manual that can be utilized practically without the text, which is reduced to a minimum. However one wonders whether the money put into these excessively numerous diagrams will not result in users who never learn much about the fishes they are identifying, and whether this money might not have been better used had it been spent on printing both a simple illustrated key (such as that in Hubbs and Lagler's "Fishes of the Great Lakes") and a little more real information on the natural history of the species. The book ends with a systematic list of the species, a list of the modern nomenclature according to Tortonese's list of Mediterranean fishes, and an index. The classification and nomenclature used by Dr. Soljan are both archaic.

It should be noted that the publishers refuse to send this and other books in the same series on regular exchange. They value it at about 10 U. S. dollars and wish to exchange it for certain specific books which they will list upon request.—GEORGE S. MYERS, *Natural History Museum, Stanford University, California.*

AMPHIBIANS OF WESTERN NORTH AMERICA. By Robert C. Stebbins. University of California Press, Berkeley and Los Angeles, California; xviii + 539 pp., 35 text-figs., 64 pls. Dec. 1951. $7.50.—This new work forms the most satisfactory and well done treatment of West American amphibians that has ever been published. Moreover, it is based largely on original work done by one of the most meticulous of present-day amphibiologists. Dr. Stebbins must be congratulated on his new book.

The work covers the amphibian fauna of Alaska, the Yukon, the Northwest Territories, British Columbia, Alberta, Saskatchewan, Washington, Oregon, Idaho, Montana, Wyoming, California, Utah, Colorado, Arizona and New Mexico, and it does it well. The illustrations, many in color and all by the author, are excellent. The treatment is by species, with the subspecies strongly subordinated, and the keys, descriptions, and general treatment of life-history, ecology and habitat are perhaps as well done as is possible in the present state of published knowledge.

The typography and general format are pleasing

although one might wish that the mere desire to be different had not induced the editors and publishers to adopt an asinine arrangement of the table of contents and a cover that positively offends a book lover. Will publishers never learn that scientific books are not sold by "cute" typographical and binding devices?

The reviewer has been studying western amphibians far longer although seldom so intensively as Dr. Stebbins, and has, as is usual in the tribe of reviewers, many points to criticize adversely. The principal one of these involves not only the present work but also most but not all of the North American herpetological handbooks that have appeared in the past twenty years. This is a nearly complete failure to give the student-user any really useful comprehension of the extra-North-American relationships of the beasts under study. It may be argued that a local handbook is no place for such extraneous matters, but the fact is that North American herpetological students almost nowhere are exposed to the herpetology of the cold, cold world outside North America. It is high time that they were, seeing that this country presumes to assume international leadership in many fields of science, and no better place can be found to begin than in a North American manual. For this one reason, the present book falls below the general level of such excellently conceived (even if far more cursory) handbooks as that of Schmidt and Davis on North American snakes.

We are reminded of this provincialism by the author's remarks on the "Scaphiopodidae" (pp. 194–195), in which he mistakes Stejneger's belief that that family name should replace Pelobatidae (on nomenclatural grounds) for a separation of the North American spadefoots into a separate family—an idea that the reviewer is sure never entered Stejneger's head. The same restricted viewpoint is again indicated by the author's quotation of Dunn ("in litt.") on the extension of the range of the Plethodontidae to the Lower Amazon, when it has been widely published, by Unterstein, Miranda Ribeiro, and Myers and Carvalho, that the range includes that area. Other examples are evident in most of the family and many of the generic accounts.

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# EDITORIAL NOTES AND NEWS

## CHLOE LESLIE STARKS

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although one might wish that the mere desire to be different had not induced the editors and publishers to adopt an asinine arrangement of the table of contents and a cover that positively offends a book lover. Will publishers never learn that scientific books are not sold by "cute" typographical and binding devices?

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